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Phylogeny and revision of genera of the subtribe
Bolitocharina (Coleoptera: Staphylinidae: Aleocharinae)¹

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ABSTRACT

A revision of the genus-level classification of the aleocharine subtribe Bolitocharina is provided. The revision is based on a phylogenetic analysis of 26 species representing all currently recognized described bolitocharine genus-level taxa as well as undescribed taxa. These were chosen from among 52 bolitocharine species examined to encompass the range of variation among them. Species-level taxa were used as terminal taxa in the phylogenetic analysis to represent the full range of structural diversity in the subtribe without making *a priori* decisions about generic assignments or taxonomic composition of genera. A character matrix of 26 taxa + outgroup by 78 derived character states (in 34 characters) was analyzed using the phylogenetic tree generating program HENNIG86. Several alternative phylogenies under different assumptions are provided. All lead to similar conclusions about generic limits. Conclusions are: (1) The subtribe Bolitocharina is shown to be monophyletic by shared possession of (a) large patch of densely arranged denticles in ventral molar area of mandibles, (b) medial setae of prementum staggered one behind the other, (c) narrow medial pseudopore field of prementum without pseudopores. (2) The genus *Ditropalia* Casey, with which many described bolitocharine genera have been synonymized, is based on plesiomorphic features and includes taxa which are not closely related. (3) The genera *Pleurotobia* Casey, *Stictalia* Casey, and *Venusia* Casey, which had been synonymized with *Bolitochara* Mannerheim, are not members of that latter genus. (4) The genus *Phymaturosilus* Roubal is a junior synonym of *Pleurotobia*. (5) The genus *Venusia* Casey is a junior synonym of *Phymatura* Sahlberg. (6) Two new genera based on undescribed species are described. These are: *Hongophila* new genus (type species *Hongophila arizonica* new species, known from the southwestern United States) and *Neotobia* new genus (type species *Neotobia alberta* new species, known from northern North America from the Rockies eastward). (7) The species *Sternotropa zealandica* Cameron is doubtfully included in the Bolitocharina. It is shown not to be a member of *Sternotropa*, which is a valid genus in the subtribe Gyrophaenina. A new genus, *Austrasilida* n. gen., is described to include it. (8) Nine monophyletic genera, including three newly described, can be recognized in a monophyletic Bolitocharina. These are *Bolitochara* Mannerheim (new synonym *Ditropalia* Casey), *Phymatura* Sahlberg (new synonym *Venusia* Casey), *Pleurotobia* Casey (new synonym *Phymaturosilus* Roubal), *Pseudatheta* Cameron, *Silusida* Casey, *Stictalia* Casey, *Hongophila* n. gen., *Neotobia* n. gen., and *Austrasilida* n. gen.

INTRODUCTION

The Bolitocharina is a subtribe of beetles in the very incompletely known staphylinid subfamily Aleocharinae. As recognized in this revision, the subtribe is composed of nine genera, in which about 70 species have been described. None of these genera has received comprehensive review, and the taxonomic status of many genera and species is uncertain. Some authors have placed nu-

merous genera and species in synonymy (for example see Fenyés, 1920; Moore and Legner, 1975; Bernhauer and Scheerpeltz, 1926; and others), especially for the North American taxa. Additionally, the subtribe has been variously treated in a broader (e.g., Bernhauer and Scheerpeltz, 1926; and Scheerpeltz and Höfler, 1948) or narrower (e.g., Fenyés, 1918) sense, further result-

ing in considerable instability in generic composition.

The subtribe Bolitocharina, as a higher taxon within the tribe Bolitocharini, has not been clearly delimited or described in detail. For this reason the genera which have been assigned to the subtribe comprise a very heterogeneous assemblage. Few genera have been adequately described and illustrations of structural features are usually not available. These factors have resulted in confusion about generic limits and assignments.

Categorical rankings of less inclusive groups of genera (subtribes) within the taxon formed by those aleocharines with 4,4,5 tarsal formula [tribe Bolitocharini—hereafter referred to as the Homalotini¹ (see Newton and Thayer, in press)] have not been stable. Various authors have raised one or more of these groups to tribal rank based on their opinion about how distinctive the included genera are in relation to other members. For example, Lohse (1974) recognized five tribes in the European fauna to include those aleocharines with a 4,4,5 tarsal formula. The lack of detailed and comprehensive studies of the higher taxa of aleocharines has contributed substantially to this instability.

I will provide evidence below that many of the taxa included in the tribe Homalotini in a traditional sense share several uniquely derived features which probably indicate that they form a monophyletic group within the Aleocharinae. I will therefore treat these less inclusive higher taxa as subtribes within the more inclusive tribe Homalotini.

This study grew out of my attempts to understand the generic composition and phylogenetic relationships among North American members of the subtribe Bolitocharina. It soon became clear that the question about phylogenetic limits of the subtribe could not be addressed in a regional context.

Therefore the study was enlarged to address the question of whether the subtribe Bolitocharina could be shown to be monophyletic based on shared derived characteristics. If so, what would be the generic composition of such a group, and what would be the phylogenetic relationships among these genera? These questions cannot be effectively addressed outside the context of the monophyly of the tribe Bolitocharini as a whole. The goal of this study is to provide a phylogenetic framework within which additional research on bolitocharines can be addressed. Though I have attempted to make it as broad based as possible (see Appendices 1, 2), its completeness is clearly limited. There are a number of probably valid bolitocharine species that I have not examined (see Taxonomic Treatment). Furthermore, the tribe Homalotini is a large, heterogeneous assemblage comprised of hundreds of described genera worldwide, some of which may be correctly placed in the subtribe Bolitocharina as here defined. A complete survey of all such taxa would be prohibitive and is outside the bounds of this study. I hope that this study will stimulate additional research on the subtribe Bolitocharina that will ultimately lead to its revision.

MATERIALS AND METHODS

The study of the phylogeny of aleocharine staphylinids has been limited by the lack of detailed comparative structural studies. The small size of most aleocharines, the large number of valid taxa, and the superficial similarity among many of these taxa, have led many workers to suggest that the group as a whole is unsuitable for serious phylogenetic study (Ashe, 1984). The error of this opinion is clear when aleocharines are examined using techniques suitable for observing the great variety of minute, but phylogenetically informative, structural features exhibited by these insects.

The basis for comparative study of microscopic structural features in the mouthparts of the Aleocharinae was laid by Sawada (1970, 1972) and was used effectively in his studies of the athetine complex of genera and species (Sawada, 1974, 1977; Yosii and Sawada, 1976). Later these character systems were used effectively and expanded upon in the study of the phylogenetic relationships and evolution of the subtribe Gyrophaeina (Ashe, 1984) and in elucidating the relationships of the aberrant genus *Tachiona* (Ashe and Wheeler, 1988). The techniques used in this

¹ Newton and Thayer (in press) have recently convincingly shown that the correct name for the tribe "Bolitocharini" should be the "Homalotini" based on priority. Consequently, the group of aleocharines characterized by 4,4,5 tarsal segmentation usually referred to as the "Bolitocharini" will be referred to as the "Homalotini," except in historical references.

study were designed to maximize the information that could be gained from microscopic characteristics.

Suitable preparation and examination of specimens are essential. Male and female specimens of species for which adequate material was available were cleared in cold, concentrated KOH, and mouthparts, aedeagi and spermathecae were dissected using techniques described in Ashe (1984). The cuticle of darkly sclerotized specimens was bleached using commercially available hydrogen peroxide to facilitate microscopic examination of the entire beetle using transmitted light. Whenever practical, the dissected parts and the body were permanently mounted under cover glasses on microscope slides using Hoyer's mounting medium. Microscope slides were then dried in a drying oven and ringed with Glyptol®. Full dissections of some taxa could not be done because of the paucity of material. In these instances, dissected parts were examined in glycerin and stored in clear glass genitalia vials pinned through the cork onto the same pin as the specimens.

Specimens were examined for general external features at magnifications up to 128× using a dissecting microscope. More detailed examination of microscopic structural features was done with a compound microscope equipped with Nomarski differential interference contrast devices. This optical system is highly recommended for study of the microstructure of small beetles. The detailed structure of many small features (especially sensory pores and similar structures), which are virtually invisible under normal light microscopy, are extremely clear under differential interference contrast optics. Drawings were made with a drawing tube.

Ashe (1984) pointed out that a broad-based comparative study of characters useful for systematic research within the Aleocharinae is not available. The variation in characters and their usefulness for taxonomic and phylogenetic analysis are unknown or at most poorly understood for most groups. This lack of knowledge cannot be remedied easily. Such a comparative base can only be developed slowly as additional detailed studies of a diversity of groups are completed. The comparative base for interpretation of characters for phylogenetic analysis in this study was a microscope slide collection of dissected aleocharines, made specifically for this and related projects, representing over 200 genera and 600 species in all major tribes and subtribes of the Aleocharinae. This breadth of coverage allows for more confident statements about the distribution of character states within the in-group and also among aleocharines as a whole. The main source of material for this slide collection was the excellent staphylinid collection of the Field Museum of Natural History in Chicago. In developing this microslide collection special attention was paid to members of the tribe Homalotini and the subtribe Bolitocharina. Members of these taxa examined

are listed in Appendices 1 and 2, respectively.

As noted above, the comparative base for this study was made possible by the excellent collection of the Field Museum of Natural History. Substantial amounts of microslide mounted and pinned material were loaned to me from this collection thanks to the generosity of Dr. Alfred Newton, Jr. This and other public and private collections that contributed material to this project and the curators responsible for the loans are:

American Museum of Natural History (AMNH), Lee H. Herman; Canadian National Collection (CNC), J. M. Campbell, A. Smetana; California Academy of Sciences (CAS), D. Kavanaugh, N. Penny; Field Museum of Natural History (FMNH), A. F. Newton, Jr.; Smithsonian Institution (USNM), T. Erwin; Snow Entomological Museum (SEM); Mr. Karl Stephan, Oklahoma (KSC); Mr. Richard Leschen, University of Kansas (RLC).

Unfortunately, repeated attempts to obtain loan of critically important bolitocharine taxa from the Natural History Museum, London, were not successful.

HISTORY OF THE SUBTRIBE BOLITOCCHARINA

Erichson (1839-1840) laid the foundation on which most subsequent taxonomic work on the subfamily Aleocharinae has been built. He established the tradition of character systems centering on the numbers of articles in the maxillary palpi, labial palpi, antennae and tarsi for recognizing higher taxa within this subfamily. Using these characters, Ganglbauer (1895) recognized 10 tribes of aleocharines. These 10 tribes, with additions and emendations, have formed the basic structure of the classification of the Aleocharinae for almost 100 years. One of these tribes, including all those genera which have the front and middle tarsi 4-segmented and the hind tarsi 5-segmented, was the Bolitocharini. Ganglbauer included 17 genera in this tribe. In spite of the similarity in tarsal structure of its members, the composition of Ganglbauer's tribe included a structurally heterogeneous assemblage of genera. The heterogeneity became more acute with discovery of additional genera with a 4,4,5 tarsal formula. By the time that Casey began his studies of the North American Staphylinidae at the turn of the twentieth century, it was clear that there were a number of distinctive subgroups within the tribe Bolitocharini. He recognized five distinctive groups which he called subtribes (Casey, 1906). Later Fenyés (1918), in summarizing knowledge of the Aleocharinae to that date, recognized 14 "Groups" within the tribe Bolitocharini which are essentially equivalent to subtribes as recognized by Casey. Though usefulness of these divisions of the Bolitocharini has not been recognized in all subsequent studies (e.g., Cameron, 1939a, b), they have formed the basis for organizing the heterogeneity among those

aleocharines with a 4,4,5 tarsal formula in most later classifications.

The first person explicitly to recognize the subtribe Bolitocharina (as the Bolitocharac) was Casey (1906). He included the described genera *Bolitochara* Mannerheim, *Phymatura* Sahlberg, *Silusa* Kraatz, *Sipalia* Mulsant and Rey, and *Leptusa* Kraatz. In addition he described five new genera: *Ditropalia*, *Stictalia*, *Silusida*, *Venusa*, and *Pleurotobia*. He recognized that these could be conveniently separated into two groups: those with an acute metasternal process and short basal segments of hind tarsi (*Silusa*, *Sipalia*, and *Leptusa*); and those with broader mesosternal processes and elongate basal segments of hind tarsi (all others). Fenyès (1918) separated the group along these lines and recognized in his group Bolitocharac (= subtribe Bolitocharina) only those taxa with broad mesosternal processes and elongate basal segments of hind tarsi. He placed *Leptusa* and *Sipalia*, along with other genera, in a new "group" the Leptusae, and *Silusa* in the Silusae. Fenyès' group Bolitocharac was similar to Casey's tribe Bolitocharac, but he synonymized several of Casey's genera with *Bolitochara* and added *Caloderina* Ganglbauer and *Gastrophaena* Fauvel. Fenyès gave no reason for synonymizing the genera *Stictalia* Casey, *Venusa* Casey, and *Pleurotobia* Casey with the European *Ditropalia* Casey. However, these synonymies have been perpetuated in all subsequent studies of the Bolitocharina.

Bernhauer and Scheerpeltz (1926) and Scheerpeltz (1934) returned to a broader concept of the subtribe. In effect, they combined Fenyès' groups Bolitocharac and Leptusae and added additional genera for a total of 19 genera in the subtribe. They also followed Fenyès' treatment of Casey's genera except they placed *Ditropalia* Casey as a subgenus of the European *Bolitochara*. Blackwelder (1944) essentially repeated this arrangement with genera found in Mexico, Central America, and South America.

This concept of the subtribe has been generally followed by most subsequent authors. Lohse (1974) treated most of the "subtribes" of the Bolitocharini as tribes. Thus his Bolitocharini is essentially the same as the subtribe Bolitocharina of previous authors. His characterization of the "tribe" Bolitocharini underscores many of the problems with this concept of the taxon. It essentially includes those taxa with 4,4,5 tarsal formula that do not have the derived features that characterize any one of the other tribal level taxa with this tarsal formula.

Seevers' (1978) revision of the North American Aleocharinae treats the subtribe Bolitocharina much as did Casey (1906), except that Seevers made no attempt to resolve the problems associated with the synonymies of Casey's genera proposed by Fenyès (1920). He accepted Fenyès' genus-level classification but admitted that some of Casey's genera may be valid. He noted that this complex of genera badly needs revision, but

generic groupings could not be considered until the male genitalia had been comparatively studied. Until such a time, he chose to recognize broader genera.

PHYLOGENETIC ANALYSIS

SYSTEMATIC POSITION OF THE SUBTRIBE BOLITOCCHARINA

When defined by 4,4,5 tarsal segmentation, the tribe Homalotini includes a large and diverse array of genera. Surprisingly, detailed examination of representatives of many of these genera (Appendix 2) has revealed several derived features which, in addition to similarity in tarsal segmentation, indicate that many of the included genera represent a monophyletic group within the Aleocharinae. These apomorphic features are (1) presence of more or less well-developed denticles in the molar region of the ventral (condylar) side of the mandible; (2) narrowing of the distance between the medial setae of the prementum so that the insertions of the setae are close or contiguous; and (3) narrowing of the medial pseudopore field so that the medial pseudopores, if present, are compressed into an irregular longitudinal row. In spite of dramatic differences in other mouthpart features (compare, for example, the maxillary and labial structures of *Silusa* and related genera with those of *Bolitochara*) and diversity of external forms, these three derived features are distributed in virtually perfect concordance with each other and 4,4,5 tarsal segmentation among most genera typically placed in the tribe Homalotini. The states of these apomorphic conditions, especially number and arrangement of molar denticles on the mandibles, vary considerably among taxa within the Homalotini. For example, molar denticles vary from large and prominent among members of *Bolitochara* to very small and indistinct in *Heterota*, or arranged in a large dense patch in *Bolitochara*, to arranged in well-separated transverse rows in *Diestota*, to arranged in more or less longitudinal rows in many *Gyrophaena*. Similar variation is exhibited to a lesser extent in other apomorphic characters. Nonetheless, considering the concordance among these features and their uniqueness within the

Aleocharinae, it seems most parsimonious to treat these variations as modifications of more basic synapomorphic conditions.

Among genera examined which have been previously placed in the Homalotini, some do not share these derived features. Of particular note in this regard are the genera *Placusa* (usually placed in the subtribe Homalotina) and *Euwira* [usually placed either in the subtribe Autaliina (e.g., Fenyès, 1918) or in its own group (e.g., Seevers, 1978, the Euvirae)]. The features that distinguish these two genera have been briefly discussed by Ashe and Kistner (1989) and in more detail by Ashe (1991). Seevers' (1978) statement that members of *Philotermes* have molar denticles appears to be incorrect; the molar regions of the specimens of this genus that I have examined are without denticles. Members of *Philotermes* also lack the other shared derived features mentioned above. Among the intertidal Phytosina, the genera *Liparocephalus*, *Diaulota*, and *Actocharis* do not have these derived features, while *Phytosus*, *Bryobiota*, and *Thinusa* do (molar denticles only very faintly present).

Naturally, many genera have not been examined in the detail necessary to evaluate fully the distribution and concordance of these characters. Nonetheless, they offer a robust first hypothesis about the monophyletic limits of the tribe Homalotini, which can be evaluated with additional study and subsequently modified if necessary.

The monophyletic nature of most of the 11 to 14 subtribes of the Homalotini, and their appropriate generic composition, has not been examined and cannot be addressed here. However, the subtribes Gyrophaenina (treated by Ashe, 1984) and the Bolitocharina (treated here) clearly represent monophyletic assemblages within this larger group. In addition, several other subtribes appear to have apomorphic features which would suggest that at least some genera assigned to them represent monophyletic groups. These include the Silusina (based on the derived condition of the maxillae and labial palpi, see Ashe and Wheeler, 1988) and the Autaliina (based on the derived structure of the ligula of the labium, see Hoebeke, 1988).

It seems most appropriate to treat each of these groups as a "subtribe" within the more inclusive "tribe" Homalotini, rather than raising each of these relatively autapomorphic subgroups to independent tribal rank as done by Lohse (1974). The latter approach is certainly legitimate in that there is no objective way to assign coordinate taxa to categories in the Linnean hierarchy; however, if these monophyletic subgroups are treated as tribes, then there is no standard category for the more inclusive monophyletic taxon. Either one would lose that level of information in the classification or one would have to create a new supertribal category. Because the subfamily Aleocharinae is presently so poorly understood phylogenetically, and substantial modification of its classification can be expected with subsequent study, I prefer a conservative approach to its classification. Since tribal rank has been often used for the more inclusive "Bolitocharini" (= Homalotini), I will continue this approach to classification which seems to provide the greatest stability in the classification while still allowing the appropriate categorical recognition of monophyletic taxa.

CHOICE OF TERMINAL TAXA

Study of the higher-level phylogeny of the Bolitocharina is seriously hampered by the instability of genus-level taxa as outlined above (see historical section). It is difficult to choose representatives of monophyletic groups as terminal taxa, since there is no evidence that any of the higher taxa are monophyletic. I therefore used species as terminal taxa for cladistic analysis without any *a priori* expectations about the limits of the genus-level taxa. The expectation was that monophyletic groups which could be recognized as genus-level taxa would become evident as a result of cladistic analysis. Terminal taxa were chosen to represent as much of the range of character variation within each traditional higher taxon as possible within the constraint of the material available for detailed study. Taxa included in the analysis share a suite of apomorphic features believed to define a monophyletic lineage. These features included: (1) mandi-

bles with large patch of densely arranged denticles in ventral molar area; (2) medial setae of prementum arranged one behind the other; and (3) medial pseudopore field of prementum narrow and without pseudopores. To avoid *a priori* decisions about the composition of genera, I have treated each described genus-level taxon whose members meet the synapomorphic criteria as outlined above as valid. I have included the type species of each of these genera except *Stictalia* (because of inadequate material for dissection) in the analysis. This helps assure that pertinent variation will not be overlooked by *a priori* decisions about generic synonymies.

Taxa included in the analysis are listed in Appendix 2. Other potential bolitocharine genera examined and found not to be part of the monophyletic Bolitocharina are listed in Appendix 1. Decisions about the possible inclusion in, or exclusion from, this analysis of the subtribe Bolitocharina of several taxa require discussion.

Sternotropa zealandica Cameron from New Zealand is included in the Bolitocharina in spite of lack of several synapomorphies that unite the remaining members of the subtribe. Structure of the labium is particularly problematic. The ligula, rather than being elongate, parallel-sided, and apically bifid as in other Bolitocharina, is short and bifid to the base (Fig. 153). More important, the medial setae of the prementum are not arranged one behind the other, but rather are on the same transverse plane. Also, the setal bases are fairly distant from one another in comparison to most other members of the tribe Bolitocharini. In conjunction with this feature, the medial pseudopore field is not greatly narrowed and retains a few pseudopores. Inclusion in the Bolitocharina is indicated by the large, well-developed patch of denticles on the ventral molar area of the mandible, which is similar to that of other Bolitocharina. In addition, the structure of the maxillae, secondary sexual characteristics, and aedeagus are all very similar to those of other Bolitocharina. Because of these similarities, I have included *Sternotropa zealandica* in the subtribe Bolitocharina for cladistic analysis, but with considerable reservation.

A second problematic genus is *Caloderina*, known only from the Palearctic *C. hierosolymitana* Saulcy. This genus was included in the "Group Bolitocharae" by Fenyès (1918-1921). This genus has a perplexing array of characteristics in comparison to the Bolitocharina. The mandibles have only a few, very tiny scattered denticles in the ventral molar area, unlike other Bolitocharina. The ligula of the labium is similar to that of the Bolitocharina and the bases of the medial setae of the prementum are close and slightly staggered one behind the other. However, the medial pseudopore field retains a few small pseudopores. The maxillae are also very similar to members of the Bolitocharina. In contrast, the terga of the abdomen of males lack the secondary sexual characteristics found in most Bolitocharina. Perhaps the most enigmatic feature of *Caloderina* is that males have a concentration of glandular and setose pores baso-medially on abdominal sternum VII. This is remarkably similar to the structure on sternum VII of *Pleurotobia* and *Bolitochara* and is not known to occur in any taxon outside of the Bolitocharina. However, males of *Caloderina* also have a broad band of pores on the base of sternum VII. Also, the apical margin of sternum VI is not modified into a projecting flap which covers this pore concentration as it is in all Bolitocharina which have such a pore structure on sternum VII.

The enigmatic distribution of synapomorphics between members of *Caloderina* and some Bolitocharina does not provide the basis for an unambiguous decision about whether *Caloderina* should be included in the subtribe Bolitocharina. I have very tentatively, and with considerable reservation, elected not to include *Caloderina* in the Bolitocharina in this study.

It is clear that either or both of the decisions to include *Sternotropa zealandica* in, and exclude *Caloderina* from, the subtribe Bolitocharina may be in error and require additional study. I have attempted to provide the basis for evaluating my decisions, and the starting point for more detailed study of the systematic positions of these two taxa, in the preceding discussion.

I have not had opportunity to examine

representatives of *Gastrophaena* Fauvel which was first included in the Bolitocharina by Fenyés (1918-1921). However, the description of this genus, as well as its occurrence with ants, leads me to believe that it is not a bolitocharine, but this proposition requires verification.

Bierig (1937) described the new subgenus *Bolitochara* (*Agaribiota*) in the genus *Bolitochara* based on the new species *B. (Agaribiota) cinctigastrea* Bierig. He states that the holotype and paratypes were placed in his collection which was ultimately deposited in the Field Museum of Natural History, Chicago. I was unable to locate specimens of this taxon among the bolitocharines in the Field Museum. However, based on the description and figures provided by Bierig (1937), it seems very unlikely that *Agaribiota* is correctly placed in the Bolitocharina. I have not included it in this analysis.

Two undescribed bolitocharine taxa included in the analysis were of uncertain generic placement. Consequently, these were tentatively assigned to "*Bolitochara*" for analysis and discussion and were subsequently appropriately assigned based on the results of the phylogenetic analysis. These are "*Bolitochara*" n. sp. A and "*Bolitochara*" n. sp. B.

CHARACTER VARIATION AND CHARACTER ANALYSIS

The most critical process in reconstruction of phylogenetic relationships among taxa is analysis of characters. This process involves two major procedures: (1) recognition and description of homologous character states, and (2) recognition of transformation series and development of hypotheses about their polarity. I agree with numerous authors (e.g., Eldredge and Cracraft, 1980; Wheeler, 1986) that *ad hoc* character weighting is highly subjective and should be used only under special circumstances. Therefore, *ad hoc* character weighting is avoided in this analysis (but see Alternative Phylogeny III), though *post hoc* character weighting in the form of "successive approximation" (Farris, 1969) is applied to the data.

Watrous and Wheeler (1981) and Maddison et al. (1984) have effectively argued that

the appropriate method for determination of polarity of transformation series is out-group comparison. This method requires that the distribution of character states be compared both among taxa in the group under analysis (in-group comparisons) and among closely and more distantly related taxa (out-group comparisons). If two states of a character occur in the in-group and only one of these states occurs in the out-group, then the state with a more restricted distribution in the in-group is the apomorphic condition. This simple instance is often not reflected in analysis, however, because of character state evolution within the out-group subsequent to the separation of in-group and out-group lineages. Out-groups may be relatively apomorphic in the characters under consideration in relation to the in-group, or some or all taxa in the out-group may have evolved relatively apomorphic states independently of, and in parallel with, members of the in-group. A single out-group is not sufficient to resolve polarity in these and similar situations, and character state comparisons across more distantly related out-groups are required to establish polarity (Maddison et al., 1984). The problems of complex character state distributions among in-group and out-group taxa is especially pertinent to this study.

Choice of appropriate out-groups for polarization of character states within the subtribe Bolitocharina is complicated by the highly autapomorphic conditions of other subtribes within the tribe Homalotini. Ashe (1984, 1986) hypothesized that the most closely related taxon to the Bolitocharina is the subtribe Gyrophaenina. Ashe (1984, 1986) discusses shared derived characters that support this relationship. Additional shared adult characters not mentioned previously that support this relationship include: (1) bases of the two medial setae of the labium modified from side-by-side to one behind the other (among gyrophaenines this is only seen in members of *Probrachida*; other gyrophaenines have lost one of the setae); (2) loss of the medial pseudopore field on the labium. Other larval characters which support this sister group relationship include: (1) reduction of the four anal hooks of the abdomen (lost in gyrophaenines), (2) the similar derived chaetotaxy of the 8th abdom-

inal segment, and (3) similarities in the tergal gland reservoir and associated gland ducts of the 8th abdominal segment (see Ashe, 1986, 1990, for details). Association of all members of both the Bolitocharina and Gyrophaenina with fresh mushrooms is possibly an additional apomorphy linking these two groups, and is in full concordance with the structural features mentioned above. However, the nature of the association with mushrooms is quite different within the two groups (Ashe, 1984, 1986, 1990; Topp, 1973).

The usefulness of the Gyrophaenina as an out-group for polarizing character states found among the Bolitocharina is seriously limited by the highly autapomorphic condition of the Gyrophaenina. The array of characters which exhibit uniquely derived states within the Gyrophaenina is extremely large (see Ashe, 1984, 1986). Polarization of these characters, as well as those for which gyrophaenines and bolitocharines share two or more states, requires comparisons across one or several more distantly related out-groups.

As noted above, *Leptusa* and related genera (Group Leptusae as recognized by Fenyès, 1918-1921) should not be included in a monophyletic Bolitocharina. They are, however, similar in many structural features. However, *Leptusa* and related genera are characterized by a number of apomorphic features in comparison to the Bolitocharina. These include: (1) reduction of eyes, loss of flight wings (and associated thoracic modifications) and reduction of the elytra by many deep-litter and soil inhabiting taxa; (2) reduction or loss of secondary sexual characteristics of males; and (3) two-segmented labial palpi. More generalized leptusines share many features with the Bolitocharina as well as other taxa within the tribe Homalotini, suggesting that they are suitable for polarizing the states of these characteristics.

As a still more distant out-group within the Homalotini, the subtribe Silusina must be considered. Silusines are highly apomorphic in mouthpart structure in relation to other bolitocharines (see Ashe and Wheeler, 1988), but some (especially *Silusa*) are very similar in male secondary sexual characteris-

tics to some members of the Bolitocharina as well as to some less specialized leptusines. This suggests that these character states, as well as others that are similarly distributed, may be relatively plesiotypic within the Bolitocharini as a whole.

Other homalotine subtribes (Homolotina, Autaliina, Phytosina, etc.) are highly derived in most pertinent structural features and offer little information useful for character analysis within the subtribe Bolitocharina.

Some members of the subtribe Bolitocharina have states of some characters that are not found among other members of the tribe Homalotini, but are widely distributed among other aleocharines. These include three-segmented labial palpi and numerous setose projections on the flabellum of the wing. In addition, some states found among members of the Bolitocharina and also scattered among taxa in related tribes are broadly distributed among other aleocharines. This distribution of character states suggests that members of the subtribe Bolitocharina retain the primitive states of these characters for which apomorphic states have been derived either uniquely or in parallel in all other members of the tribe Homalotini. Therefore, polarization of these characters must be done by using the Aleocharinae as a whole as an outgroup.

In spite of the preceding discussion, problems in polarity of characters resulting from lack of a uniquely and clearly defined out-group only become apparent in a few transformation systems (Characters 1, 5, 10). These problems and my tentative resolutions are discussed under the appropriate characters.

Use of such a hierarchy of out-groups to polarize characters within the subtribe Bolitocharina is not very satisfying. However, a more concisely delimited out-group cannot be recognized at the present time. This highlights the fact that a careful character analysis within almost any large group of aleocharines is limited by our superficial understanding of characters, character states, and their distribution within this diverse assemblage of organisms. I hope that the character analysis presented below and the phylogenetic diagram based on it will

stimulate additional studies to test it as well as provide a base on which other studies in the Aleocharinae can be built. A summary of characters and states analyzed here is presented in Appendix 3.

Character 1. Head: Shape.—States of this character among bolitocharines form a more or less continuous series which can be arbitrarily divided into five states: (0) head distinctly broader than long (width : length ratio 1.1 or greater); (1) head more or less oval, slightly broader than long (width : length ratio $>1.0(1.1)$ (Fig. 28); (2) head more or less quadrate or round (width : length ratio about 1.0) (Fig. 132); (3) head slightly elongate (width : length ratio $(1.0)0.9$) (Fig. 96); (4) head distinctly elongate (width : length ratio 0.9 or less) (Fig. 7). Relatively broad heads (width : length ratio 1.1 or greater) are widely distributed among the Gyrophaenina, more generalized Leptusina and some Silusina as well as other Aleocharinae. Based on this, condition 0 above is considered the plesiotypic condition and the transformation series is arranged in a linear series of decreasing head width ($0=1=2=3=4$). It is reasonable to assume that this transformation has occurred many times independently.

Alternative hypotheses about polarity of this character would focus on the relatively quadrate heads of many *Leptusa* and some gyrophaenines as well as many other bolitocharines. This condition could be considered to be plesiomorphic. If so, the transformation series would be bidirectional, head width increasing in one direction and decreasing in the other. However, a relatively broad head appears to be the more generally distributed condition. Also, a quadrate head appears to be associated with other derived body proportions in *Leptusa* and others. Therefore, this latter hypothesis is less parsimonious than the former.

Character 2. Head: Infraorbital Carina.—Only two states of this character are recognized among bolitocharines: (0) infraorbital carina moderate to strong, complete; and (1) infraorbital carina absent, except faintly evident near maxilla. A well-developed infraorbital carina is widely distributed among all outgroups. Therefore state 0 is considered the plesiotypic condition. A single transformation series from presence of an intraorbital carina to loss is indicated ($0=1$).

Character 3. Head: Neck.—Three states of this character are recognized among bolitocharines: (0) neck absent (Fig. 81); (1) neck present but slightly developed (neck wider than $2/3$ head width) (Fig. 22); and (2) neck present, distinct to very distinct (neck $2/3$ to $1/2$ head width) (Fig. 7). Head without a neck is the condition found among most gyrophaenines, most leptusines, and silusines as well as many other aleocharines. Therefore, state 0 is considered to be the plesiotypic condition. A transformation series reflecting progressive constriction of the base of the head into a neck is indicated ($0=1=2$).

Character 4. Head: Setation.—Three states of this

character can be recognized among bolitocharines: (0) setae directed medially in postero-lateral areas and anteriorly in midline and anterior portions of head; (1) most to all setae directed anteriorly; and (2) most to all setae directed medially. State 0 is found among many gyrophaenines, leptusines, and silusines as well as many other aleocharines. However, within each of these groups, one can also find members which exhibit the other states. The general distribution of state 0 suggests that this is the plesiotypic condition. However, polarity of this character is not strongly supported. A bidirectional transformation series is indicated, one direction of modification leading to all setae directed anteriorly and an independent modification leading to all setae directed medially ($1=0=2$).

Character 5. Pronotum: Width : Length Ratio.—Although the states of this character form a more or less continuous series within the Bolitocharina, gaps in the distribution of relative widths of the pronota among members suggest that the character distribution can be conveniently divided into three states: (0) width : length ratio = 1.4 or greater (Fig. 80); (1) ratio = $>1.2(1.4)$ (Fig. 110); and (2) ratio = 1.2 or less (Fig. 6). Relatively wide pronota (width : length ratio greater than 1.4) are widely distributed within the Gyrophaenina and Silusina, and are found among some Leptusina. This is also a widely distributed feature among other aleocharines, where it is usually associated with other pronotal features generally considered to be relatively plesiotypic. Given this distribution, state 0 is hypothesized to be plesiotypic. A transformation series of decreasing width : length ratio is indicated ($0=1=2$).

Character 6. Pronotum: Width of Pronotum Relative to Width of Base of Elytra.—The range of this character within the Bolitocharina can be conveniently divided into two states: (0) pronotal base as wide or virtually as wide as base of elytra (Fig. 80); and (1) pronotal base distinctly narrower than base of elytra (Fig. 6). State 0 is the condition found among most members of all of the out-groups, and is hypothesized to be the plesiotypic condition. A transformation series involving narrowing of the pronotum in relation to the elytra is indicated ($0=1$).

Character 7. Pronotum: Microsculpture.—Three states of this character are recognized: (0) integument with slight to moderate reticulate microsculpture; (1) integument with obsolete microsculpture; and (2) integument smooth and shining, without a trace of microsculpture. Most members of the out-groups (especially leptusines) and many other aleocharines have reticulate integumental microsculpture. Therefore state 0 is hypothesized to be plesiotypic. A transformation series involving progressive loss of microsculpture is indicated ($0=1=2$).

Character 8. Wing: Average Number of Setose Projections on Flabellum.—The number of setose projections on the flabellum of the wing varies from 0 to 13 within the Bolitocharina, yet is relatively constant within a given taxon. This character

varies more or less continuously when the Bolitocharina are considered as a unit. The total range can be divided more or less arbitrarily into five states: (0) 10-13 setose projections on flabellum (Fig. 57); (1) $4 \leq 8$ (Fig. 140); (2) $\geq 3 \leq 4$ (Fig. 124); (3) $> 1 < 3$ (Fig. 89); (4) 1 or less (Fig. 104).

This character represents one of the most enigmatic in terms of polarity of any in the Bolitocharina. The flabellum of the wing is a small lobe at the base from which arise elongate setose projections. Reduction in number of such projections is associated with general reduction in size of the flabellum. Within the tribe Homalotini the presence of a flabellum with setose projections is extremely rare outside of the subtribe Bolitocharina. Notably they are absent from the wings of all gyrophaenines, leptusines, and most silusines. Among the Homalotini that I have examined, I have found them to be present only in some members of the genus *Silusa* (3-5 projections per flabellum). If out-group comparison were made only among subtribes within the Homalotini then the polarity would have to be hypothesized to be from absence of a setose flabellum to origin and enlargement of the flabellum. However, presence of a well-developed flabellum with 10-15 setose projections per wing is widely, if erratically, distributed among other aleocharines. For example, Sawada (1977) noted the occurrence of these structures and the variation in number of setose projections among some athetine aleocharines. This suggests that members of the Bolitocharina may retain the primitive condition of presence of a well-developed flabellum, as they appear to do in the instance of three-articled labial palpi. The alternative hypothesis, that presence of a flabellum among the Bolitocharina represents a reversal from absence to presence with subsequent enlargement, is also possible, and is more consistent with the condition in more closely related out-groups. However, I tentatively accept the hypothesis that the presence of a well-developed flabellum (state 0) among bolitocharines is the plesiotypic condition, with subsequent reduction of the flabellum within the lineage ($0 \Rightarrow 1 \Rightarrow 2 \Rightarrow 3 \Rightarrow 4$). This implies that other lineages within the Homalotini have independently lost the flabellum.

Character 9. First Visible Abdominal Tergum: Direction of Setae.—Two conditions are recognized among the Bolitocharina: (0) all setae directed posteriorly; and (1) some setae directed obliquely or transversely toward the midline. State 0 is the condition found among most members of all outgroup taxa and most other aleocharines. Therefore state 0 is hypothesized to be plesiomorphic and a unidirectional transformation is indicated ($0 \Rightarrow 1$).

Character 10. Mesosternum: Medial Carina.—Three states may be recognized among the Bolitocharina: (0) medial carina strong, complete to apex of mesosternal process (Fig. 14); (1) medial carina strong but fading in apical 0.5-0.2 of mesosternum (Fig. 56); (2) medial carina present

only on basal 0.2-0.3 of mesosternum (Figs. 88, 123). A strong, complete mesosternal carina is widely distributed among taxa in all out-groups and most other aleocharines. Therefore, state 0 is hypothesized to be the plesiotypic condition with progressive reduction of the carina apically as the more derived condition ($0 \Rightarrow 1 \Rightarrow 2$).

Character 11. Intercoxal Processes: Degree of Separation of Middle Coxae.—This character can be divided into three relatively arbitrary states: (0) coxae narrowly separated, by less than 0.15 times total length of meso- and metasternal processes (Fig. 103); (1) coxae moderately separated, by more than 0.15 times and less than 0.35 times combined length of meso- and metasternal processes (Fig. 35); (2) coxae widely separated, by more than 0.35 times combined length of meso- and metasternal processes (Fig. 56). Polarization of this transformation series is not clear. Gyrophaenines and some silusines (e.g., *Diestota*) have broadly separated mesocoxal cavities. However, leptusines, most silusines, and most other aleocharines have narrowly separated mesocoxae. I tentatively accept the hypothesis that narrowly separated mesocoxae are plesiotypic among bolitocharines. This implies the assumption that the wide separation of mesocoxae of gyrophaenines is derived independently from that condition in bolitocharines. This hypothesis about polarization of this character should be applied with considerable caution; however, it implies a transformation series of enlargement of the meso- and metasternal processes and subsequent widening of the distance between the mesocoxae ($0 \Rightarrow 1 \Rightarrow 2$).

Character 12. Intercoxal Processes: Isthmus Present or Absent.—Three states in relative length of the isthmus between the meso- and metasternal processes can be conveniently recognized: (0) isthmus distinctly present (length greater than 0.1 times combined length of meso- and metasternal processes plus isthmus) (Fig. 103); (1) isthmus slight (visible isthmus length between 0.1 and 0.02 times combined length of processes plus isthmus) (Fig. 75); and (2) visible isthmus virtually to completely absent (meso- and metasternal processes in contact or separated by no more than 0.02 times their combined length) (Fig. 56). Problems with unambiguous polarization of this series of character states directly parallel those discussed under Character 11. A very few gyrophaenines have a very slight isthmus (Ashe, 1984) but most have contiguous meso- and metasternal processes. Most other out-group taxa have distinctly visible isthmuses. I tentatively accept the hypothesis that state 0 is the plesiotypic condition for the same reasons as noted for Character 11. Likewise, the same caution in application of this polarity hypothesis is implied. A transformation direction of increasing approximation of the meso- and metasternal processes is indicated ($0 \Rightarrow 1 \Rightarrow 2$) by this polarity.

Character 13. Antenna: Antennomere 4.—Three states are recognized: (0) antennomere 4 similar

in setation, microsculpture and general shape to antennomeres 5-10; (1) antennomere 4 transitional in setation, microsculpture and general shape between antennomeres 1-3 and 5-10; and (2) antennomere 4 similar in setation, microsculpture and general shape to antennomeres 1-3. State 0 is widely distributed among all out-group taxa except gyrophaenines, among which it is the condition exhibited only by a few relatively plesiotypic taxa (see Ashe, 1984). State 0 is therefore hypothesized to be plesiotypic. Ashe (1984) previously discussed the distribution of this character among gyrophaenines, which do not exhibit intermediate conditions of antennomere 4, and were relatively easy to assign to one or the other of the extreme states. However, some bolitocharines exhibit an intermediate condition which requires an additional state (state 1) in this analysis. The transformation series indicated is toward progressive modification of antennomere 4 to be more similar to antennomeres 1-3 ($0 \Rightarrow 1 \Rightarrow 2$).

Character 14. Antenna: Relative Lengths of Articles 5-10.—Three states of this character can be recognized among bolitocharines: (0) articles 5-10 progressively decreasing in relative lengths apically; (1) articles 5-10 more or less the same in relative lengths; and (2) articles 5-10 distinctly increasing in relative lengths toward the apex. State 0 is the condition found among leptusines, silusines and all but a very few more highly derived groups of gyrophaenines. It is also a condition which is widely distributed among other aleocharines. State 0 is therefore hypothesized to be the plesiotypic condition. A transformation series toward increasing lengths of the apical antennomeres is indicated ($0 \Rightarrow 1 \Rightarrow 2$).

Character 15. Mandibles: Molar Denticles.—Only a single state of this character is found among members of the subtribe Bolitocharina. Comparison of this character among bolitocharines and out-groups reveals two recognizable states at this level of analysis: (0) denticles in molar region few to numerous, scattered, not densely arranged; and (1) denticles very numerous, arranged densely in a large patch (Figs. 10, 31, 52). State 0 is found in all members of the tribe Homalotini except the subtribe Bolitocharina (but the exact arrangement of the denticles varies among higher taxa). State 0 is considered to be plesiotypic, and state 1 is synapotypic for the subtribe Bolitocharina ($0 \Rightarrow 1$).

Character 16. Maxillary Lacinia: Inner Apical Teeth.—Four states of this character can be recognized among the bolitocharines: (0) one row of teeth on inner face of the lacinia in apical 0.25-0.35 (Fig. 53); (1) inner face of apical 0.25 of lacinia with one row of teeth more basally and two irregular rows more apically (Fig. 137); (2) inner face of lacinia with 3-6 rows of teeth in apical 0.25, with a noticeably denser concentration of teeth near apex (Figs. 12, 54); and, (3) 3-6 rows of teeth in apical 0.25 with a very dense and large concentration of teeth near apex (Fig. 151).

Members of the Leptusina, Silusina, and most other aleocharines have a single inner row of teeth in the apical 0.25-0.35. Gyrophaenines have highly autapomorphic lacinial apices, which have been modified into dense patches of spines which function as spore brushes (see Ashe, 1984). Comparisons with gyrophaenines are not appropriate for resolution of the polarity of this character. However, the very general distribution of state 0 among other out-groups indicates that this is the plesiomorphic condition. If this hypothesis of polarity is accepted, then a transformation series of increasing number of teeth on the inner face of the lacinia, especially near the tip is indicated ($0 \Rightarrow 1 \Rightarrow 2 \Rightarrow 3$).

Character 17. Labium, Ligula: Pair of Sensory Spines.—Three states of this character can be recognized: (0) pair of large, prominent sensory spines on ligula (Fig. 55); (1) pair of sensory spines on ligula minute to small (Fig. 138); and (2) sensory spines absent from ligula (Fig. 102). Some gyrophaenines, most leptusines, and many silusines have a prominent pair of sensory spines on the ligula. These have been reduced or are absent among many gyrophaenines. Nonetheless, the hypothesis that state 0 is plesiotypic is most parsimonious. A transformation series involving increasing reduction of this pair of spines is suggested ($0 \Rightarrow 1 \Rightarrow 2$).

Character 18. Labium: Medial Setae.—Five states of this character can be recognized among members of the subtribe Bolitocharina and related bolitocharines: (0) medial setae side by side, bases close to contiguous; (1) medial setae side by side anterior to medial pseudopore field, bases distant (Fig. 153); (2) medial setae arranged one laterally behind the other in medial pseudopore field, bases close to contiguous (Fig. 74); (3) medial setae arranged one directly behind the other, bases close (Fig. 122); and (4) medial setae arranged one directly behind the other, bases distant (Fig. 102). Virtually all members of the tribe Homalotini except the subtribes Bolitocharina and Gyrophaenina have state 0. Most other aleocharines have state 1. In addition, within the subtribe Bolitocharina, *Sternotropa zealandica* exhibits state 1. This latter species shares so many other features with members of the subtribe Bolitocharina that it seems most parsimonious to hypothesize that this relatively plesiotypic condition for aleocharines as a whole is secondarily derived in this lineage. Members of the subtribes Bolitocharina and Gyrophaenina are unique among aleocharines as far as is known in sharing the condition that the bases of the medial setae are placed one behind the other. Most gyrophaenines have in addition lost one of the setae. Since state 0 is widespread within the tribe Homalotini, it is hypothesized to be the primitive condition for this analysis. State 1 is treated as an independent evolution of a relatively plesiotypic condition. States 2, 3, and 4 are hypothesized to represent a transformation series involving increasing displacement of one medial seta behind

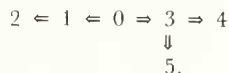
the other. A bidirectional transformation series is indicated ($1 \rightleftharpoons 0 \rightleftharpoons 2 \rightleftharpoons 3 \rightleftharpoons 4$).

Character 19. Labium: Medial Pseudopore Field.—Three states may be recognized among members of the Bolitocharina and closely related out-groups: (0) medial pseudopore field narrow, pseudopores present in a linear array; (1) medial pseudopore field more or less broad, pseudopores present in a more or less rectangular array (Fig. 153); and (2) medial pseudopore field narrow, pseudopores absent (Figs. 74, 122). State 0 is widely distributed among all members of the tribe Homalotini except the subtribes Bolitocharina and Gyrophaenina. As in Character 18, only *Sternotropa zealandica* shares character 1 with most alcocharines outside of the Homalotini. For the same reasons as noted under Character 18, I hypothesize that this condition in *S. zealandica* represents secondary evolution to a more plesiotypic condition. Members of the subtribes Bolitocharina and Gyrophaenina share state 2, though the medial pseudopore field is wider among gyrophaenines than among bolitocharines. State 0 is hypothesized to be the plesiotypic condition in relation to the condition found among the Bolitocharina (state 2) as well as in relation to the secondary derivation of a more plesiotypic condition in *S. zealandica* (state 1). A bidirectional transformation series is indicated ($1 \rightleftharpoons 0 \rightleftharpoons 2$).

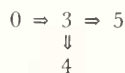
Character 20. Male Secondary Sexual Characteristics: Elytra, Sutural Carinae.—Three conditions are recognized among the Bolitocharina: (0) elytral suture not modified; (1) each elytron with a small knob or tubercle near the suture in posterior 0.5; (2) each elytron with a distinct and strong carina near the suture in posterior 0.5. The condition among most numbers of all out-groups is state 0. Based on this distribution, state 0 is hypothesized to be the plesiotypic condition. The presence of a small sutural knob in a very few members of North American *Leptusa* does not seem sufficient to hypothesize that state 1 is the plesiotypic condition. State 2 is found only among some members of the subtribe Bolitocharina. A unidirectional transformation series is indicated ($0 \Rightarrow 1 \Rightarrow 2$).

Character 21. Male Secondary Sexual Characteristics: Tergum VII.—A great variety of male secondary sexual characters can be found on abdominal tergum VII of bolitocharines. These can be divided into six states: (0) small to moderate medial tubercle, without lateral scattered asperities (Fig. 39); (1) small to very small medial tubercle, with small to very small lateral asperities (Fig. 105); (2) without medial tubercle, with very faint scattered asperities (Fig. 111); (3) with short distinct medial carina (Fig. 144); (4) with very long, prominent medial carina (Fig. 45); (5) with two to three oblique carinae on each side of midline (Fig. 60). State 0 is found among many gyrophaenines, leptusines which retain secondary sexual characteristics, and many silusines. None of the other conditions are widely distributed among the out-

groups. Therefore state 0 is hypothesized to be the plesiotypic condition. The diversity of states suggests a complex character state tree within the transformation series. I hypothesize two independent directions of modification. One direction is characterized by increase in lateral asperities followed by reduction of the medial tubercle, and ultimately loss of secondary sexual characteristics except for very faint scattered asperities ($0 \Rightarrow 1 \Rightarrow 2$). The alternative direction of modification is characterized by enlargement of the medial tubercle to a carina and subsequent enlargement of this carina ($0 \Rightarrow 3 \Rightarrow 5$). Origin of state 4 (two to three oblique carinae on each side) within this transformation series is uncertain. I tentatively hypothesize that it is a modification of state 3 by progressive division of the medial carina, but there is little direct evidence for this. This is the only resolution of the origin of this state that is concordant with the more confident resolution of Character 22. While this is a weak justification, it is more parsimonious than creating a known discordant character state distribution. The following transformation series is indicated.



Character 22. Male Secondary Sexual Characteristics: Tergum VIII.—The diversity of male secondary sexual characteristics on abdominal tergum VIII parallels that of abdominal tergum VII. Six states can be recognized: (0) small to very faint medial tubercle (Fig. 39); (1) a few minute, scattered asperities (Fig. 105); (2) no modifications (Fig. 111); (3) short medial carina (Fig. 144); (4) prominent long medial carina (Fig. 45); (5) moderate to prominent medial carina with shorter flanking carinae or tubercles (Fig. 60). Resolution of the polarity of states of this character is directly analogous to that of Character 21. State 0 is the only one of the states found among bolitocharines that is generally distributed among the out-groups. Therefore, state 0 is hypothesized to be plesiotypic. Two independent directions of modification are indicated. One direction of transformation involves loss of secondary sexual features ($0 \Rightarrow 1 \Rightarrow 2$). The other direction involves enlargement of the medial tubercle to form a carina which becomes more prominent and develops secondary carinae on each side, as indicated thus.



State 5 is hypothesized to be derived from state 3 rather than state 4 because of the greater similarity of the carina in state 5 to that of state 3 than to that of state 4.

Character 23. Male Secondary Sexual Characteristics: Tergum VIII, Denticles in Apical Emargination.—The

posterior margin of the eighth tergum is broadly emarginate in most bolitocharines. The depth of the emargination and the development of the denticles in the emargination vary among taxa. Three states can be recognized: (0) emargination broad and deep, denticles moderate to robust (Fig. 60); (1) emargination broad and shallow, denticles very small to faint (Fig. 39); and (2) emargination very shallow to indistinct, denticles virtually absent (Fig. 111). Polarization of the states of this character is not immediately evident. Gyrophaenines have a great diversity of modifications of the apical margin of tergum VIII of males, but none of these seem directly homologous with the modifications found among bolitocharines. All three states can be found among leptusines. Among silusines, *Silusa* has state 0. The presence of state 0 in a very few *Leptusa* and *Silusa* provides the basis for the hypothesis that this is the plesiotypic condition. If correct, then the presence of states 1 and 2 among both bolitocharines and leptusines would indicate independent reduction of male secondary characteristics in these two groups. An unidirectional transformation series is indicated within the Bolitocharina ($0 \Rightarrow 1 \Rightarrow 2$).

Character 24. Male Secondary Sexual Characteristics: Sternum VI, Lobate Projection Apicomedialely.—Males of some taxa of Bolitocharina have a small, lobate projection medially on the apical border. This projection may be glabrous or setose. Three states are recognized: (0) lobate projection absent (Figs. 38, 76, 90); (1) lobate projection present, glabrous (Figs. 16, 17, 125, 126); (2) lobate projection present, setose (figs. 58, 59). This lobate projection is not found in any taxa outside of the Bolitocharina. Therefore state 0 is the plesiotypic condition. The setae in state 2 are clearly highly modified. Their presence is hypothesized to be derived in comparison with a glabrous lobe. A unidirectional transformation series is indicated ($0 \Rightarrow 1 \Rightarrow 2$).

Character 25. Male Secondary Sexual Characteristics: Sternum VII, Medial Setose Glandular Area.—Males of the Bolitocharina and most males of other subtribes in the Homalotini have a band of many hundreds of asetose sensory pores extended around the basal margin of sternum VII. These are clearly evident under compound microscope examination, especially with differential interference optics. Males of some bolitocharines have in addition to this band of pores, a medial concentration of sensory pores from which arise modified setae. Some also have rugose surrounding areas which appear to be evaporative surfaces. Three states of this character can be recognized: (0) uniform broad band of asetose sensory pores present around base of sternum VII, medial setose glandular concentration absent (Figs. 37, 76, 90, 106); (1) band of asetose sensory pores around base of sternum VII broad, medial setose glandular concentration present but small (Fig. 125); and (2) band of asetose sensory pores around base of sternum VII reduced, me-

dial setose glandular concentration present, large (Figs. 16, 59). As noted above most males of the tribe Homalotini (including many Bolitocharina) have a band of asetose pores at the base of sternum VII. This band may be quite broad and contain hundreds of pores. Males of some species also have such a band on the bases of other sterna. States 1 and 2 only occur in some groups of Bolitocharina (except for *Caloderina*, see discussion under subtribe Bolitocharina above). State 0 is hypothesized to be plesiotypic. A single unidirectional transformation series is indicated ($0 \Rightarrow 1 \Rightarrow 2$).

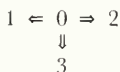
Character 26. Male Secondary Sexual Characteristic: Sternum VIII, Apical Triangular Lobe.—Two states of this character are recognized: (0) margin of lobe setose to edge (Figs. 16, 58, 125); and (1) lobe with distinct asetose margin (Figs. 38, 90, 106, 141). Males of many Homalotini have the posterior margin of sternum VIII modified into a prominent triangular projection. This projection is also present in some females, but it is always much broader and far less prominent in females. Some males of the subtribe Bolitocharina have an asetose margin on the triangular lobe. Since state 0 occurs in all out-groups (except the Gyrophaenini, in which this triangular lobe occurs in greatly reduced state in only a few taxa) and also in some members of the Bolitocharina, state 0 is hypothesized to be plesiotypic. A single transformation is indicated ($0 \Rightarrow 1$).

Character 27. Male Genitalia: Apical Lobe of Aedeagus.—Shape of the apical lobe of the aedeagus varies considerably among members of the Bolitocharina, but five distinctive forms can be recognized: (0) apical lobe large, tentlike (Figs. 21, 62, 66, 93); (1) apical lobe slender and elongate (Figs. 41, 46, 79); (2) apical lobe slender, rather foot-shaped in lateral aspect (Figs. 107, 114); (3) apical lobe slender, recurved (Fig. 112); and (4) apical lobe bifid (Fig. 146). A large, rather tentlike apical lobe is the condition found among some gyrophaenines and most leptusines and silusines, though within each of these taxa the apical lobe has been variously modified independently. Two basic directions of modification are indicated. In one the apical lobe is modified into a slender, elongate structure ($0 \Rightarrow 1$). In the other the apical lobe is modified into a slender, footlike structure with subsequent modification of the footlike apex into a recurved structure ($0 \Rightarrow 2 \Rightarrow 3$). The position of state 4 in this transformation series is uncertain. I am taking a conservative position and hypothesizing that it arose independently from state 0 ($0 \Rightarrow 4$), but it may be an intermediate form between states 0 and 2. Alternatively, it may have been independently derived from state 2, though this hypothesis would be highly discordant with other characters. A tridirectional transformation series is indicated.

$$\begin{array}{c}
 1 \leftarrow 0 \Rightarrow 2 \Rightarrow 3 \\
 \downarrow \\
 4
 \end{array}$$

Character 28. Male Genitalia: Aedeagus, Internal Plates.—Three states can be recognized among the Bolitocharina: (0) internal plates present, plates large, flattened (Figs. 21, 62, 66); (1) internal plates present, plates spinose and recurved (Fig. 128); (2) internal plates absent (Figs. 41, 46, 79, 93). All leptusines and silusines have a pair of large, flattened plates within the median lobe. These are absent from all gyrophaenine median lobes; however, this condition is most parsimoniously hypothesized to be derived independently from the similar condition in Bolitocharina. Based on this distribution, state 0 is hypothesized to be plesiotypic. Two independent directions of modification are likely. In one direction the plates are modified into spinose structures. Alternatively, the plates may be lost. A bidirectional transformation series is indicated ($1 \Leftarrow 0 \Rightarrow 2$).

Character 29. Male Genitalia: Median Lobe, Flagellum.—The length and shape of the flagellum of the aedeagus varies considerably among the Bolitocharina. Four states of the flagellum can be recognized: (0) moderate length, tubular (Figs. 21, 62); (1) short tubular (Fig. 112); (2) very long, tubular (Figs. 107, 114); (3) moderate length, tapering to sharp apex (Figs. 41, 46, 128). State 0 is found among many gyrophaenines, leptusines, and silusines and this is hypothesized to be the plesiotypic state. No clear morphocline is evident that would link any of the other states together into a transformation series. Therefore, each apotypic state is hypothesized to have originated independently from the plesiotypic condition.



Character 30. Female Spermatheca: Basal Bulb Shape.—Three conditions of the basal bulb are here recognized: (0) basal bulb simple, base rounded (Figs. 19, 24); (1) basal bulb elongate, rounded at base (Fig. 131); and (2) basal bulb simple, with small knob at base (Fig. 109). State 0 is found among most members of all out-group taxa, and is therefore hypothesized to be the plesiotypic condition. States 1 and 2 do not appear to be parts of a single transformation series, and are here hypothesized to have arisen independently from the plesiotypic condition ($1 \Leftarrow 0 \Rightarrow 2$).

Character 31. Female Spermatheca: Neck Shape.—Three conditions of the deflection of the spermathecal neck can be recognized among the Bolitocharina: (0) neck straight to very slightly bent (Fig. 94); (1) neck bent at more than a 30° angle and less than a 90° angle (Figs. 24, 63); and, (2) neck bent at more than a 90° angle (Fig. 109). State 0 is widespread among gyrophaenines, leptusines and silusines and is hypothesized to be plesiotypic. States 1 and 2 can be most parsimoniously arranged in a transforma-

tion series of increasing deflection of the spermathecal neck ($0 \Rightarrow 1 \Rightarrow 2$).

Character 32. Female Spermatheca: Tube Structure.—Two states can be recognized: (0) tube membranous (Figs. 24, 42); (1) spermathecal tube sclerotized (Fig. 109). State 0 is the condition in most bolitocharines and all members of the out-group, and is hypothesized to be the plesiotypic condition. State 1 is limited to a few members of the Bolitocharina. A transformation from unsclerotized to sclerotized spermathecal tube is indicated ($0 \Rightarrow 1$).

Character 33. Female Spermatheca: Tube Shape.—Three states can be recognized among the Bolitocharina: (0) spermathecal tube of moderate length, more or less straight (Fig. 24); (1) spermathecal tube very long and irregularly convoluted (Figs. 43, 130); and (2) spermathecal tube twisted into 1 to 3 distinct loops (Fig. 109). State 0 is found among most members of the Bolitocharina as well as being widely distributed among the out-groups. State 0 is therefore hypothesized to be the plesiotypic condition. States 1 and 2 do not appear to be parts of a single transformation series, and are here hypothesized to have arisen independently from the plesiotypic condition ($1 \Leftarrow 0 \Rightarrow 2$).

Character 34. Female Sexual Characteristics: Vaginal Sclerotization.—Many members of the Bolitocharina have a circular sclerotized area in the vagina. The spermathecal duct opens into the membranous areas near the center of this sclerotized area. The sclerotized ring may be complete and very distinct, or only partially complete and slightly sclerotized. Three states can be recognized among the Bolitocharina: (0) vaginal sclerotization very lightly sclerotized, absent or present as an inconspicuous arc (Fig. 43); (1) vaginal sclerotization moderately to slightly sclerotized, evident as approximately 0.5 circle of sclerotized area (Fig. 24); and (2) vaginal sclerotization moderately to well sclerotized, sclerotized ring complete or at least 0.75 complete (Figs. 63, 94, 143). A sclerotized vaginal ring, either partial or complete, is not found among the out-groups. Therefore, state 0 is hypothesized to be the plesiotypic condition. States 1 and 2 can be most parsimoniously arranged in a transformation series of increasing sclerotization of the vaginal ring ($0 \Rightarrow 1 \Rightarrow 2$).

CLADISTIC ANALYSIS

Additive binary coding of character states was used for the states of each character. This coding method was required for two reasons: (1) many character transformation series included more than one derived state; and (2) complex character state trees involving transformations in two or more directions from the plesiotypic condition are

indicated for some characters. Additive binary coding allows for accurate representation of such multidirectional transformations within a character state matrix. The additive binary code for each character state is shown in Appendix 3. This produces a matrix of 78 potentially derived character states representing 34 separate characters. All character states are coded for 26 bolitocharine taxa. In addition, a hypothetical out-group is constructed in which all character states are set to the plesiomorphic condition, and this group is inserted into the matrix. Missing data for some characters and some taxa resulted from the fact that both sexes were not available for dissection for all taxa and/or the particular characters were not observable on the specimens available for a variety of reasons. These missing data are coded in the matrix as a "?". The resulting character state matrix of 27 taxa (including out-group) by 78 characters is shown in Table 1.

Character state data were analyzed using the phylogenetic tree generating program HENNIG86 version 1.5 (Farris, 1988). Analysis options provided for generation of several initial trees produced by addition of terminal taxa in different sequences, followed by branch-swapping on each of these trees (option "hennig*"), and extended branch swapping with retention of all shortest possible trees (option "bb*"). Additional phylogenetic patterns were examined by successive approximation (Farris, 1969), a technique which relies on *post hoc* character weighting according to the fit of each character to the available shortest trees. This procedure is provided for in the HENNIG86 program by the options "xs w, cc" which will calculate the weights of the characters and list their weights. This option was used successively on each set of generated shortest trees until character weights no longer changed, indicating stability in the trees. Farris (1969) has shown that this technique will clarify phylogenetic pattern even in data sets which exhibit considerable homoplasy. Shortest trees were combined into their most general mutually consistent branching pattern by generation of a Nelson consensus tree.

Initial unweighted analysis of the data

yielded 58 shortest trees with a length of 189, a consistency index of 0.38, and a retention index of 0.72. A Nelson consensus tree of these shortest trees revealed that phylogenetic pattern was poorly resolved for many taxa (Fig. 1). The phylogeny resulting from unweighted analysis is characterized by a large basal multichotomy. Three monophyletic groups are resolved [*Pleurotobia* + *Phymaturosilusa*, *Bolitochara* (including *Ditropalia*), and *Stictalia*]. However, species of *Silusida*, *Venusa*, all *Phymatura*, *Pseudatheta*, "*Bolitochara*" n. sp. A, "*Bolitochara*" n. sp. B, and "*Sternotropa*" *zealandica* are all parts of the single basal multichotomy.

Successive approximation required five iterations to reach stability in character weights. This resulted in nine shortest trees, each with a consistency index of 0.69 and a retention index of 0.90. A Nelson consensus of these nine shortest trees showed excellent resolution of branching pattern with unresolved nodes appearing only in a few terminal taxa (Fig. 2). Decisions about generic limits are based primarily on this tree, although alternatives will be presented later. Therefore, I will discuss the structure of this tree in some detail.

The Major Lineages.—The subtribe Bolitocharina is shown to be monophyletic by two apomorphic features by which inclusion in the subtribe was determined (see above) (characters 15-1, mandibles with dense patch of molar denticles, and 18-2-4, medial labial setae with bases arranged one behind the other). In addition, four other apomorphic features are concordant with these: characters 8-1, wings with $>4 \leq 8$ setose projections on flabellum; 10-1, mesosternum with strong carina that fades in apical 0.5-0.3; 12-1, intercoxal process with slight isthmus; and, 31-1, female spermatheca with neck bent $>30^\circ < 90^\circ$. Character states 8-1 and 10-1 at this level in the analysis require reversals of these characters to the plesiotypic condition at other levels on the tree. The analysis, and the consensus tree, require that the states of several characters be treated as though they are ambiguous at this level on the tree (13-2,1; 13-1,0; 17-1,0; 31-1,0).

The phylogenetic tree of bolitocharine rela-

Table 1. Primitive (0) and derived (1) states of 34 character systems for an outgroup and 26 taxa of the subtribe Bolitocharina.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34		
State	4321	1	21	12	21	1	21	4321	1	21	21	21	21	21	1	321	21	1432	12	21	45321	54312	21	21	1	4321	12	321	21	21	1	12	21			
Outgroup	0000	0	00	00	00	0	00	0000	0	00	00	00	00	00	00	0000	00	0000	00	0000	00000	00	00	00	00	0000	00	0000	00	00	00	00	00	00	00	
Pleurotobia	0000	0	00	00	00	0	00	0000	0	00	11	11	00	1	011	00	0111	01	11	01100	10100	00	11	11	0	0000	00	0000	00	00	00	00	00	00	00	11
sp. A	0000	0	00	01	00	0	00	0000	0	01	11	00	00	1	011	00	0111	01	11	01100	10100	00	11	11	0	0000	00	0000	00	00	00	00	00	00	00	11
trimaculata	0000	0	00	01	00	0	00	0000	0	01	11	00	00	1	011	00	0111	01	11	01100	10100	00	11	11	0	0000	00	0000	00	00	00	00	00	00	00	11
Phymatosilusa	0000	0	00	00	00	0	00	????	0	01	11	00	00	1	011	00	0111	01	11	01100	10100	00	11	11	0	0000	00	0000	00	00	00	00	00	00	00	11
magnifica	0000	0	00	00	00	0	00	????	0	01	11	00	00	1	011	00	0111	01	11	01100	10100	00	11	11	0	0000	00	0000	00	00	00	00	00	00	00	11
Silusida	0000	0	00	00	00	0	00	0111	0	11	00	01	01	00	1	001	01	0111	01	00	00000	00000	00	00	00	1	0000	01	001	00	00	00	00	00	00	11
marginella	0000	0	00	00	00	0	00	0111	0	11	00	01	01	00	1	001	01	0111	01	00	00000	00000	00	00	00	1	0000	01	001	00	00	00	00	00	00	11
"Bolitochara"	0000	0	00	00	00	0	00	0001	0	11	01	01	11	01	1	000	00	0111	01	00	00000	00000	00	00	00	1	1000	01	010	00	01	0	00	11	00	11
n. sp. B	0000	0	00	00	00	0	00	0001	0	11	01	01	11	01	1	000	00	0111	01	00	00000	00000	00	00	00	1	1000	01	010	00	01	0	00	11	00	11
n. sp. A	0000	0	00	00	00	0	00	0001	0	01	00	01	11	00	1	000	01	0111	01	01	00001	00001	00	01	01	0	0001	10	100	01	01	0	10	00	00	11
Venusia	0000	0	00	00	00	0	00	0001	0	11	01	11	11	11	1	000	11	0011	01	00	10100	01100	00	00	00	1	0001	01	100	00	01	0	10	01	00	11
blanchardi	0000	0	00	00	00	0	00	0001	0	11	01	11	11	11	1	000	11	0011	01	00	10100	01100	00	00	00	1	0001	01	100	00	01	0	10	01	00	11
Phymatura	0000	0	00	00	00	0	00	0011	0	01	01	11	11	11	1	000	01	0111	01	00	00100	00000	00	00	00	1	0001	01	100	00	00	00	00	00	00	01
brevicollis	0000	0	00	00	00	0	00	0011	0	01	01	11	11	11	1	000	01	0111	01	00	00100	00000	00	00	00	1	0001	01	100	00	00	00	00	00	00	01
picta	0000	0	00	00	00	0	00	????	0	00	01	11	11	11	1	???	??	????	01	00	00100	00000	00	00	00	?	0001	01	100	??	??	??	??	??	??	??
jucunda	0000	0	00	00	00	0	00	????	0	00	01	11	10	11	1	???	??	????	01	01	00100	00100	00	00	00	?	0001	01	100	??	??	??	??	??	??	??
Stictalia	0011	0	00	00	01	0	00	1111	0	01	00	01	11	00	1	011	11	0111	01	00	00011	00011	01	00	00	1	0110	01	001	10	11	1	01	01	01	
brevicornis	0001	0	00	00	01	0	00	222?	1	01	00	01	11	00	1	011	11	0111	01	00	00001	00001	01	00	00	1	0110	01	001	10	11	1	01	01	01	
nigra	0011	0	00	00	01	0	00	1111	1	01	00	01	11	00	1	011	11	0111	01	00	00001	00001	01	00	00	1	0110	01	001	10	11	1	01	01	01	
minor	0011	0	00	00	01	0	00	1111	1	01	00	01	11	00	1	011	11	0111	01	00	00001	00001	11	00	00	1	0110	01	001	10	11	1	01	01	01	
californica	0011	0	00	10	01	1	01	1111	0	01	00	01	11	00	1	011	11	0111	01	00	00001	00001	01	00	00	1	0010	01	010	10	11	1	01	00	00	
rugipennis	0111	0	00	10	01	1	11	1111	0	01	00	01	11	00	1	011	11	0111	01	00	00001	00001	01	00	00	1	0010	01	010	10	11	1	01	00	00	
sp. 3	0111	0	00	10	01	1	11	222?	0	01	00	01	11	00	1	011	11	0111	01	00	00001	00001	01	00	00	1	0010	01	010	10	11	1	01	00	00	
unicolor	0111	0	00	10	11	1	11	222?	0	00	00	01	11	00	1	011	11	0111	01	00	00011	00011	11	00	00	1	0010	01	010	10	11	1	01	00	00	
sp. 6	0111	0	00	10	01	1	01	1111	1	00	00	01	11	00	1	011	11	0111	01	00	00001	00001	11	00	00	1	0010	01	010	10	11	1	01	00	00	
bakeri	0011	0	00	10	01	1	00	0111	0	00	00	01	11	00	1	011	11	0111	01	00	00001	00001	01	00	00	1	0010	01	010	10	11	1	01	00	00	
Bolitochara	1111	0	00	00	11	1	11	0001	0	00	01	11	00	00	1	000	00	0001	01	11	10100	00011	00	01	11	0	0000	00	010	00	11	0	00	01	00	
(D.) bella	0011	1	11	01	11	1	11	0001	0	00	11	01	00	00	1	111	01	0111	01	11	10100	01100	01	01	11	0	0000	00	001	00	11	0	00	01	00	
(s.s.) lucida	0011	1	11	01	11	1	11	0011	0	00	11	01	00	00	1	111	01	0111	01	11	10100	01100	01	01	11	0	0000	00	001	00	11	0	00	01	00	
(s.s.) lunulata	0111	1	11	01	11	1	11	0011	0	00	01	11	00	00	1	111	00	0111	01	11	10100	01100	01	01	11	0	0000	00	001	00	11	0	00	01	00	
(D.) mulsanti	0111	0	11	00	11	1	11	0001	0	00	01	01	00	00	1	011	00	0111	01	11	10100	00001	00	01	11	0	0000	00	001	00	??	??	??	??	??	
(D.) obliqua	0111	0	01	01	11	1	11	0001	0	00	01	11	00	00	1	011	01	0111	01	00	00011	00011	11	01	11	0	0000	00	001	00	01	0	00	01	00	
Pseudatheta	0011	0	00	01	00	0	11	1111	0	11	00	11	00	01	1	000	01	0001	01	11	?????	00000	00	00	00	0	0001	01	100	??	??	??	??	??	??	
elegans	0001	0	00	10	00	0	11	1111	1	00	11	11	00	1	111	11	1000	10	00	?????	00011	00	00	00	0	0000	01	010	00	01	1	00	11	00	11	
"Sternotropa"	0001	0	00	10	00	0	11	1111	1	00	11	11	00	1	111	11	1000	10	00	?????	00011	00	00	00	0	0000	01	010	00	01	1	00	11	00	11	
zealandica	0001	0	00	10	00	0	11	1111	1	00	11	11	00	1	111	11	1000	10	00	?????	00011	00	00	00	0	0000	01	010	00	01	1	00	11	00	11	

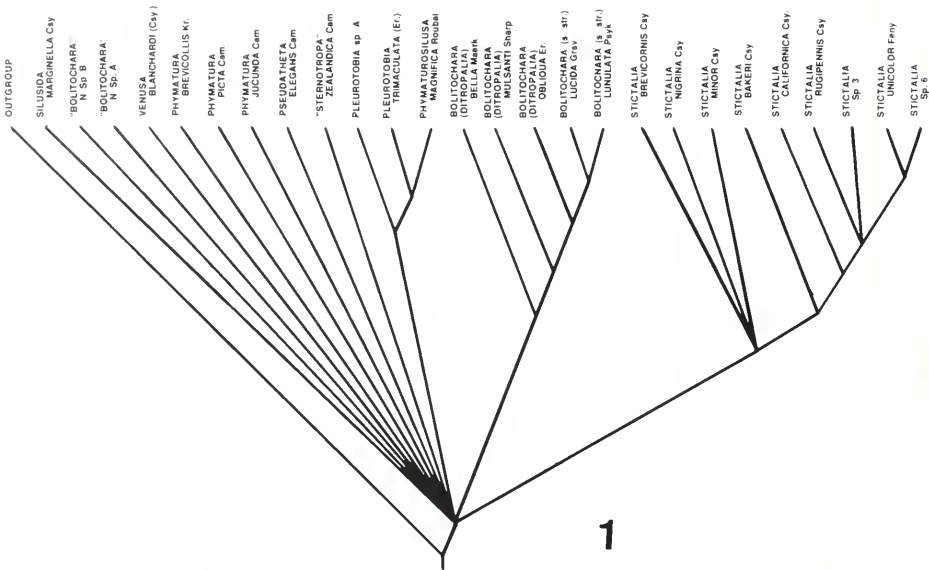


Fig. 1. Phylogeny of bolitocharine taxa. All taxa included; without successive approximation. Nelson consensus tree of 58 shortest trees. Length = 189; C.I. = 0.38; R.I. = 0.72.

tionships splits basally into two main lineages. For convenience of discussion I provide informal names for these lineages. The “*Bolitochara* lineage” includes species that have at various times been placed in the following four genera: *Phymatosilusa*, *Pleurotobia*, *Bolitochara*, *Ditropalia*, and an undescribed species designated as “*Bolitochara*” n. sp. A. The “*Stictalia* lineage” includes species which have been variously placed in five genera: *Phymatura*, *Venusa*, *Silusida*, *Pseudatheta*, *Stictalia*, as well as the aberrant *Sternotropa zealandica* and an undescribed species here designated “*Bolitochara*” n. sp. B for analysis.

The “*Bolitochara* lineage” is hypothesized to represent a monophyletic lineage based on three shared derived conditions in the male secondary sexual characteristics: 20-1, male elytra with a small knob or carina near suture in posterior 0.5; 24-1, male sternum VI with medial lobate projection; and; 25-1, male sternum VII with baso-medial concentration of setose glandular pores and corresponding reduction of broad band of asetose pores around base of sternum. These three features, especially 24-1 and 25-1, offer robust evidence of the monophyly of this lineage. These features are unique to the Aleocharinae as far as is known (but see discussion about *Caloderina* above). There

can be no reasonable doubt about the derived condition of these character states. Additionally, the complex nature of these structures and their similarity among all taxa provide strong evidence for homology. Since characters 24-1 and 25-1 are consistently found together in all bolitocharines in which they occur, it could be argued that they form a functional complex which evolved together. Consequently, they might be treated as a single character. However, the structures are located on different areas of adjacent sterna, and at this point functional correlation is only presumed, not demonstrated. Most important, treating these two characters as a single character would not alter their robust support for the monophyly of the “*Bolitochara* lineage.”

The most basally derived lineage, and the sister group to all other taxa in the “*Bolitochara* lineage,” is the species designated “*Bolitochara*” n. sp. A. Members of this species (and presumably other members of this lineage) differ from other members of the “*Bolitochara* lineage” by derived features of the aedeagus, male secondary sexual characteristics, and spermatheca (see descriptive section for details). In addition, it lacks many of the derived features which characterize other members of the “*Bolito-*

reversal: 11-2, intercoxal processes wide, separating coxae greater than 0.35 times the combined width of the coxae; 16-1, maxillary lacinia with one row of inner apical teeth more basally and two or more irregular rows apically; 21-5, male tergum VII, with two to three oblique carinae on each side of midline; 22A-5, male tergum VIII with moderate to prominent medial carina flanked by shorter carinae or tubercles (includes state 22-3, male tergum VIII with short medial carina); 24-2, male sternum VI with lobate projection setose; 34-2, female vaginal sclerotization moderate to distinct (0.75-1.00 complete ring of sclerotized tissue); and 8-0 (reversal 8-1 \Rightarrow 8-0), wing with 10 to 13 setose projections on flabellum. The relationships among the three taxa combined by these synapomorphies cannot be resolved by characters used in the analysis. They are very similar in general habitus, male secondary sexual features, aedeagus, and spermatheca. A further derived similarity among these taxa which is not included in the analysis is that males of all three taxa have relatively longer antennal articles than females. Specimens of *Phymatosilusa* differ from those of *Pleurotobia* primarily in that the lateral carinae on terga VII and VIII of male *Phymatosilusa* are greatly reduced; the most lateral ones are absent to virtually absent in many instances.

The sister lineage to the *Pleurotobia-Phymatosilusa* lineage is one which includes members of the genera *Ditropalia* (usually treated as a subgenus of *Bolitochara*) and *Bolitochara*. This lineage is hypothesized to be monophyletic based on six synapomorphies and one reversal: 1-3, head shape slightly elongate (width : length ratio $< 1.0 < 0.9$); 5-2, pronotum relatively narrow, width : length ratio 1.2 or less; 6-1, pronotum distinctly narrower than elytra; 7-2, pronotum without microsculpture, integument smooth and shining; 21-4, male tergum VII with very large medial carina; 22-2, male tergum VIII with no secondary sexual features; and 10-0 (reversal 10-1 \Rightarrow 10-0) medial carina of mesosternum strong, complete to apex of process. Although none of these characters is particularly striking and none offers robust confirmation of the monophyly of this lineage, the

number of concordant derived characteristics shared by all of the taxa on this lineage is strong evidence of monophyly.

An important feature of the *Ditropalia-Bolitochara* lineage is that the three species of *Ditropalia* (usually treated as a subgenus of *Bolitochara*), *D. bella*, *D. obliqua* and *D. mulsanti*, do not appear to represent a monophyletic group. In fact, *D. mulsanti* shares a number of derived features with members of *Bolitochara* (s. str.) and *D. obliqua* (3-1, neck present, slightly developed, neck width greater than 2/3 head width; 16-2, inner face of maxillary lacinia with 3 to 6 rows of teeth in apical 0.25 with noticeably denser concentration of teeth near apex; and, 29-1, median lobe of aedeagus with short, tubular flagellum). No evidence exists for the monophyly of *Ditropalia*. This will be discussed more fully in a later section of this paper.

Ditropalia obliqua and the two species of *Bolitochara* are hypothesized to form a monophyletic group based primarily on two unambiguous shared derived characteristics: 4-1, almost all head setae directed anteriorly (a condition derived independently in some *Stictalia*), and 23-1, male tergum VIII with broad shallow apical emargination with denticles very small to faint. The monophyly of these three species in relation to *Ditropalia mulsanti* is not strongly supported by these characters. However, the lineage which includes all examined species of *Bolitochara* (s. str.) (*B. lunulata* and *B. lucida*) forms a monophyletic group based on eight shared derived features. Most important among these are: 2-1, infraorbital carina absent except faintly present near maxillary insertion; 3-2, neck present, narrow, width 2/3 to 1/2 head width; 16-3, inner apical teeth of maxillary lacinia with 3 to 6 rows of teeth in apical 0.25 and very dense and large concentration of teeth near apex; 22-4, male tergum VIII with very long prominent medial carina; 31-2, neck of spermatheca bent at greater than a 90° angle. These characters show that these taxa of *Bolitochara* are highly derived in relation to the taxa of *Ditropalia* examined. However, as noted above, *Ditropalia* does not appear to represent a monophyletic group in relation to *Bolitochara*.

Sister lineage to the "Bolitochara lin-

age" is the "Stictalia lineage." The "Stictalia lineage" is hypothesized to represent a monophyletic group based on five shared derived features at this level of the cladogram: 13-1, antennomere 4 transitional in setation between 1-3 and 5-10; 17-1, sensory spines of ligula minute to small; 26-1, apical triangular lobe of male sternum VIII with a distinct asetose margin; 28-2, median lobe of aedeagus without internal plates; and 34-1, sclerotization of female vagina moderate to slight, present as approximately 0.5 circle of sclerotized cuticle. Of these synapomorphies, characters 26-1 and 28-2 provide the strongest evidence of monophyly. Character 26-1 is unique as far as I know within the Aleocharinae. Character 28-2 represents a loss; however, the concordance of this character with 26-1 and others suggests that the loss of internal plates in the median lobe of the aedeagus is probably homologous among all members of this lineage.

The most basally derived lineage of the "Stictalia lineage" unites all examined species of *Phymatura*, *Venusia* and "*Bolitochara*" n. sp. B into a monophyletic group. These taxa share three unambiguous shared, derived traits: 11-1, middle coxae moderately separated, intercoxal processes width $>0.15<0.35$ times combined width of coxae; 13-2, antennomere 4 similar to 1-3; and 14-1, antennomeres 5 to 10 more or less similar in relative lengths (relative lengths of antennomeres neither increasing or decreasing). These are not particularly strong characters, and they are made weaker by the fact that all of them are derived independently in other parts of the "*Stictalia*" lineage. The monophyly of this lineage cannot be considered strongly supported. However, the alternative placement of "*Bolitochara*" n. sp. B on the sister lineage near *Silusida* is also unsatisfactory.

The species designated "*Bolitochara*" n. sp. B is an aberrant taxon. It is clearly not a member of any monophyletic and previously recognized genus-level taxon. In addition to lacking the synapomorphies which define the lineage that includes all *Phymatura* and *Venusia* as a monophyletic group (see below), it exhibits uniquely derived characteristics in the aedeagus, and a derived reversal in the

large number of setose projections on the flabellum of the wing (6-8).

The genera *Phymatura* and *Venusia* are shown to be a monophyletic unit based on five shared derived characteristics; 12-2, isthmus of intercoxal processes virtually to completely absent, (shared with some members of the "*Bolitochara*" lineage as well as being homoplasous within the "*Stictalia*" lineage); 14-2, relative lengths of antennomeres 5 to 10 distinctly increasing in relative lengths toward the apex of the antenna; 17-1, pair of sensory spines on ligula minute to small; 21-3, male tergum VII with short distinct medial carina; and 21-1, apical lobe of aedeagus slender and elongate. It is not possible to show that *Venusia* is monophyletic in relation to *Phymatura* with available data. Instead, *Venusia* appears to be a member of the monophyletic genus *Phymatura*.

The sister lineage to the *Phymatura-Venusia*-"*Bolitochara*" n. sp. B lineage includes all members of the genera *Silusida*, *Pseudatheta*, "*Sternotropa*" *zealandica*, and *Stictalia*. This lineage is hypothesized to be monophyletic based on three synapomorphies: 8-3, $>1<3$ setose projections on flabellum of wings; 16-1, maxillary lacinia with one row of teeth more basally and two or more irregular rows more apically; and 17-2, pair of sensory spines absent from ligula of labium. The most basally derived taxon in this lineage is *Silusida*. The genus *Silusida* is unique in the structure of the aedeagus and the very short, incrassate antenna with strongly transverse antennomeres.

The sister lineage to the *Silusida* includes "*Sternotropa*" *zealandica*, *Pseudatheta*, and *Stictalia*. Eleven derived conditions are shared by members of these three taxa. However all but three of these are ambiguous (resolved as at least two possible states) at this level on the consensus tree. The three unambiguous synapomorphies are: 1-1, head shape oval (width : length = $>1.0<1.1$); 8-4, one or less setose projections on the flabellum of the wing; and 32-1, tube of female spermatheca sclerotized (reversed in *Pseudatheta* and "*Sternotropa*"). Evidence for the monophyly of this lineage, and probably the entire "*Stictalia*" lineage, is complicated by the presence of "*Sternotropa*" *zealandica* within this lineage. While this is undoubtedly the most parsimo-

nious position for "*Sternotropa*" *zealandica*, it is so aberrant within the Bolitocharina (see discussion under "Choice of Taxa" above) that its presence seriously complicates character state distributions throughout the tree (see Alternative Phylogenies).

The lineages "*Sternotropa*" *zealandica* + *Pseudatheta* and all *Stictalia* are hypothesized to be sister lineages. The lineage "*Sternotropa*" + *Pseudatheta* is the most enigmatic on the tree. As noted above, the character state distributions on this lineage are seriously confused by the aberrant nature of "*Sternotropa*" *zealandica*. Of the 12 character states which form the basis for recognition of this lineage, eight are represented by ambiguous states of the characters and two represent reversals to plesiotypic conditions. The two remaining unambiguous derived character states which imply monophyly for this lineage are: 7-2, pronotum microsculpture absent, integument smooth and shining; and 12-2, intercoxal processes with isthmus virtually to completely absent. Both of these are derived in parallel in other parts of the tree. Therefore, the evidence for a sister group relationship between "*Sternotropa*" *zealandica* and *Pseudatheta* is highly suspect. This doubt is only enhanced by the dramatic differences between members of these two taxa. In spite of this most parsimonious resolution of relationships, I seriously doubt if they are closely related. The problem seems to be with the position of "*Sternotropa*." It appears that this taxon is placed with *Pseudatheta* simply because it will not fit anywhere else on the tree with any parsimony. The evidence of the sister group relationship is primarily negative rather than the positive possession of shared derived characters.

All species of *Stictalia* included in the analysis group into a single lineage which is hypothesized to be monophyletic based on 11 shared derived character states: 1-2, head shape more or less quadrate (width : length = about 1.0); 5-1, pronotum width : length ratio $>1.2 < 1.4$; 13-2, antennomere 4 similar to 1-3; 15-2, inner face of maxillary lacinia with 3 to 6 rows of teeth in apical 0.25 and noticeably denser concentration of teeth near apex; 21-1, male tergum VII with small to very small medial tubercle and small to very small lateral asperities; 22-2, male tergum

VIII with no modifications; 23-1, denticles in apical emargination of male tergum VIII very small to faint; 27-2, median lobe of aedeagus with apical lobe slender, foot-shaped in lateral aspect; 30-2, basal bulb of spermatheca with small knob at base; 31-2, neck of female spermatheca bent at $>90^\circ$ angle; and 33-2, tube of spermatheca twisted into 1 to 3 regular loops. Many of these character states are unique to this group of species within the Bolitocharina. These shared derived conditions provide strong evidence that the species of *Stictalia* represent a monophyletic group.

Two monophyletic lineages within *Stictalia* can be recognized. These are recognized most readily by the dramatic differences in their aedeagal structure. These correspond to the groups that I tentatively recognized as *Stictalia* type I and *Stictalia* type II. Interestingly, these groups were shown to be monophyletic in this analysis. *Stictalia* type I (characterized by *Stictalia brevicornis* Casey), including three species (*S. brevicornis*, *S. nigrina*, *S. minor*) in this analysis, is hypothesized to be monophyletic based on: 27-3, medial lobe of aedeagus with apical lobe slender, recurved; and 29-1, flagellum of median lobe short, tubular. *Stictalia* type II (characterized by *Stictalia californica* Casey and including *S. notata*, the type species of *Stictalia*), including six species (*S. californica*, *S. rugipennis*, *S. bakeri*, *S. unicolor*, *S. sp. 3*, *S. sp. 6*) in this analysis, is hypothesized to be monophyletic based on three shared derived states and one derived reversal: 4-1, most or all head setae directed anteriorly; 6-1, pronotum distinctly narrower than elytra; 29-2, flagellum of aedeagus very long, tubular; and 34-0 (reversal 34-1 = 0) female vaginal sclerotization very slight, sclerotized portion absent or present only as an inconspicuous arc. In addition to the apomorphies indicated by this analysis, these two different groups of *Stictalia* can be easily recognized externally by differences in color pattern, punctuation and male secondary sexual characteristics.

ALTERNATIVE PHYLOGENIES

Because of the uncertainties about inclusion of "*Sternotropa*" *zealandica* in the Bolito-

charina (see discussion under "Choice of Taxa"), "*S.*" *zealandica* was removed from the data matrix and a series of alternative phylogenies computed. The same algorithm and options were used as in the previous computations.

Alternative Phylogeny I.—The first phylogeny is based on computation of all shortest trees without weighting and without successive approximation. Two shortest trees were produced with a length of 181, a consistency index of 0.41 and a retention index of 0.75. A Nelson consensus of these two trees (Fig. 3) has a number of features which are different from the previous preferred tree (Fig. 2). "*Bolitochara*" n. sp. A is shown to be sister to all other Bolitocharina in the analysis. All other Bolitocharina are divided into two lineages: a *Stictalia-Silusida* lineage and a lineage which includes all others. One very dramatic difference is that "*Bolitochara*" n. sp. B and all species of *Phymatura*, *Venusia*, and *Pseudatheta* are on a lineage with *Pleurotobia* and *Bolitochara* rather than with *Stictalia*. Another difference is that the members of *Phymatura* do not group into a single monophyletic group. This seems unlikely to be a correct representation of phylogeny because all members of *Phymatura*+*Venusia* share unique derived features in the aedeagus. This cladogram is similar to that in Figure 2 in that *Phymaturosilusa* is a member of *Pleurotobia*, and *Pleurotobia* and *Bolitochara* (+*Ditropalia*) are each shown to be monophyletic and sister groups to each other.

Alternative Phylogeny II.—The second phylogeny produced without "*S.*" *zealandica* involved successive approximation on the two trees produced in Alternative Phylogeny I. Five consecutive runs were required before character weights reached stability. Six shortest trees were produced with a length of 479, a consistency index of 0.67 and a retention index of 0.89. A Nelson consensus of these six trees (Fig. 4) produced only a single major difference from Alternative Phylogeny I. That is, all members of *Phymatura*+*Venusia* united into a single monophyletic group. This is similar to the preferred phylogeny (with "*Sternotropa*" *zealandica*, Fig. 2). The overall structure of the consensus tree is similar to that of Alternative Phylogeny I: "*Bolitochara*"

n. sp. A is sister to all other bolitocharines; there are two main lineages—a *Silusida-Stictalia* lineage, and a "*Bolitochara*" n. sp. B-*Phymatura* (+*Venusia*)-*Pseudatheta*-*Pleurotobia* (+*Phymaturosilusa*)-*Bolitochara* (+*Ditropalia*) lineage. The most dramatic difference between Alternative Phylogeny II and the preferred phylogeny (Fig. 2) is the inclusion of "*Bolitochara*" n. sp. B, *Phymatura*, *Venusia*, and *Pseudatheta* on a lineage with *Pleurotobia* and *Bolitochara* rather than *Stictalia*.

Alternative Phylogeny III.—If the states of Characters 24 (male sternum VI with lobate projection medially) and 25 (male sternum VII with medial setose glandular area) are each given an ad hoc weight of 3, then 38 shortest trees are produced with a length of 191, a consistency index of 0.43 and a retention index of 0.78. A Nelson consensus of these 38 trees (Fig. 5) is very similar to that of the preferred tree (Fig. 2). It differs only in that *Pseudatheta* is placed as a part of a basal trichotomy rather than as a member of the lineage which includes *Stictalia*. This ad hoc weight does not seem unreasonable because the derived states of these characters are virtually unique within the Aleocharinae.

In summary, it is clear that the presence of "*Sternotropa*" *zealandica* within the Bolitocharina has a dramatic effect on the phylogenetic analysis. This effect is reflected primarily in modifications of the composition of major lineages when "*S.*" *zealandica* is eliminated from the analysis. In spite of the differences between the alternative phylogenies (Figs. 3, 4, 5) and the preferred phylogeny (Fig. 2), it is striking that the compositions of monophyletic lineages above the basal branches remain the same throughout. For example, in all analyses, members of *Pleurotobia*+*Phymaturosilusa*, *Phymatura*+*Venusia*, *Bolitochara* (including *Ditropalia*) and *Stictalia*, are united as monophyletic lineages. In addition, *Silusida*, *Pseudatheta*, "*Bolitochara*" n. sp. A and "*B.*" n. sp. B are consistently treated as monophyletic lineages rather than as members of other genus-level taxa. New characters and additional analyses will be required to resolve conflicts in the composition of basal lineages. However, the present analyses provide a solid base for delimiting monophyletic

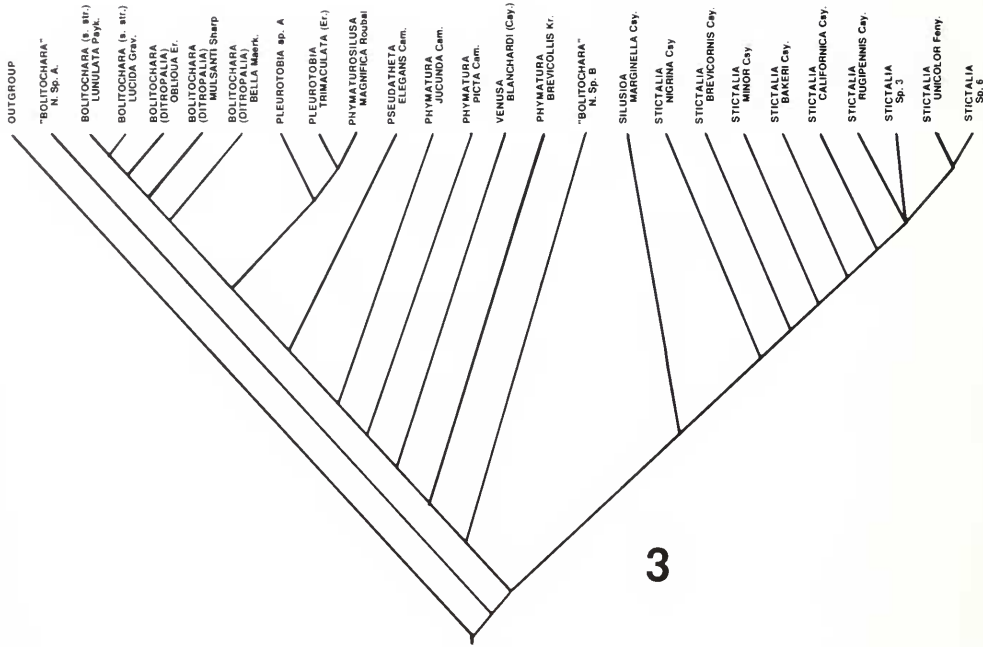


Fig. 3. Alternative phylogeny I of bolitocharine taxa. "*Sternotropa*" *zealandica* Cam. excluded; without successive approximation. Nelson consensus tree of two shortest trees. Length = 181; C.I. = 0.41; R.I. = 0.75.

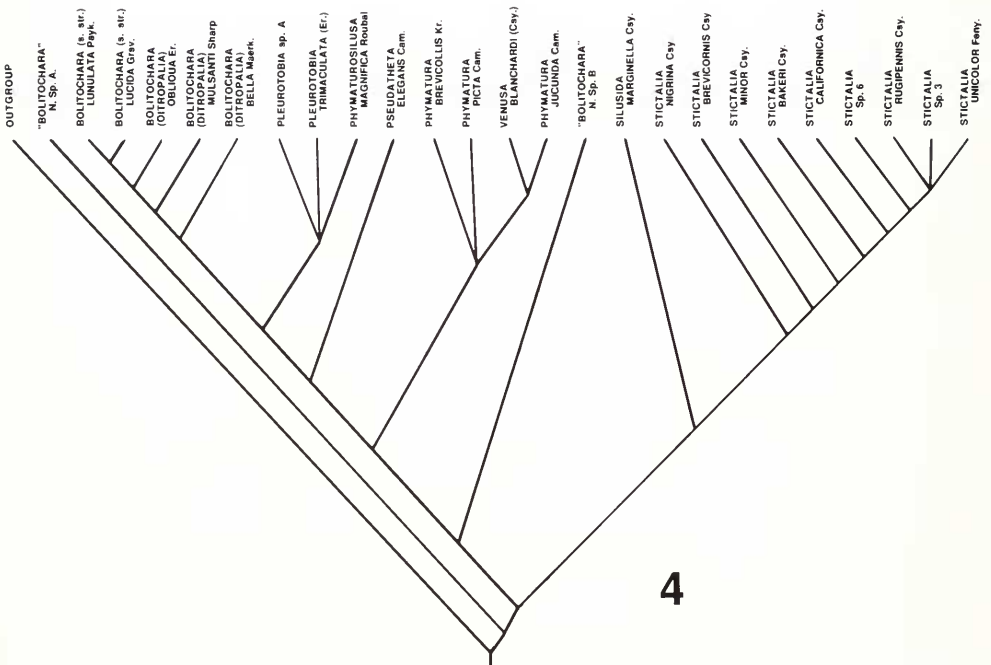


Fig. 4. Alternative phylogeny II of bolitocharine taxa. "*Sternotropa*" *zealandica* Cam. excluded; with successive approximation. Nelson consensus tree of six shortest trees. Length = 479; C.I. = 0.67; R.I. = 0.89.

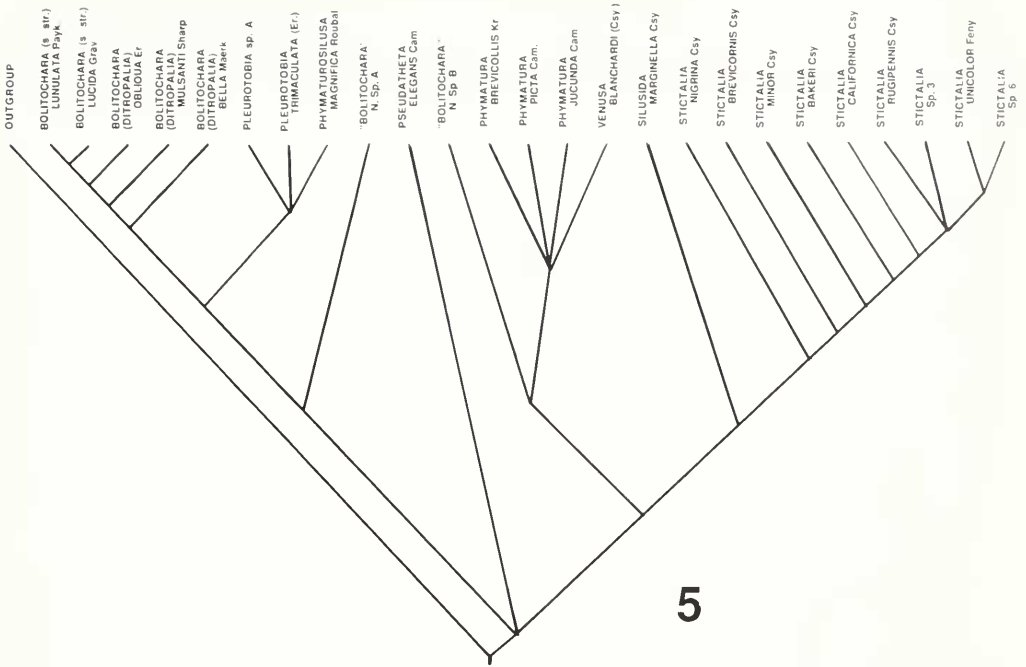


Fig. 5. Alternative phylogeny III of bolitocharine taxa. “*Stenotropa*” *zealandica* Cam. excluded; without successive approximation; with characters 24 and 25 each given an *ad hoc* weight of “3.” Nelson consensus tree of 38 shortest trees. Length = 191; C.I. = 0.43; R.I. = 0.78.

genus-group taxa within the Bolitocharina.

TAXONOMIC CONCLUSIONS
BASED ON CLADISTIC ANALYSIS

Since there is good evidence that the members of the subtribe Bolitocharina as here recognized form a monophyletic group, there are two possible approaches to categorical ranking. Firstly, since many of the included taxa have previously been synonymized with the genus *Bolitochara*, one could consider the entire subtribe to represent one genus. The correct name of this genus would be *Bolitochara*. Monophyletic groups within this genus could be treated as subgenera. Alternatively, one could continue to assign the entire monophyletic lineage to the subtribal category, as presently done, and treat each of the monophyletic subunits as a genus. Within the context of the cladistic analysis these alternative treatments of categorical assignment are equivalent in that each conveys the same cladistic information. There are no completely objective criteria which would allow one to choose between

them. Under these circumstances, one must choose between the two ranking systems based on other criteria, such as historical precedent, nomenclatorial stability and efficient storage and retrieval of information, as long as application of these criteria does not obscure or violate the cladistic information about monophyletic lineages.

I have elected to follow the second of the rankings systems. In effect, this results in the entire lineage being assigned to the subtribal category and each demonstrably monophyletic lineage which has previously had a generic name assigned to one or more of its members being assigned to the genus category. This requires that three taxa be assigned to newly described monotypic genera. Two of these include only previously undescribed species, and one represents a new assignment (see below).

I have chosen this alternative for ranking of taxa for the following reasons: (1) most of the monophyletic lineages include one or more taxa which have previously been placed in described genera. Therefore, there

are valid genus-group names available for most monophyletic lineages. (2) The structural diversity within the subtribe is substantial. (3) Genera previously synonymized with *Bolitochara* were synonymized and placed in the subgenus *Ditropalia* based on plesiotypic characteristics and do not represent a monophyletic group. (4) Several distinctive lineages (e.g., *Phymatura*, *Silusida*) have never been synonymized with *Bolitochara*. (5) If coordinate sister groups should be given equal categorical rank, then the monophyletic "Bolitocharina" must be given the same rank as its sister group, the subtribe Gyrophaenina. While there are also valid reasons for assigning the entire monophyletic lineage to the genus *Bolitochara* (the alternative ranking method), I believe that these are no more compelling than those supporting the rankings that I have chosen.

The fate of described genus-level taxa and other appropriate monophyletic groups as a result of the cladistic analysis and the ranking criteria chosen are discussed below.

Bolitochara Mannerheim.—The International Commission of Zoological Nomenclature (1961, Opinion 599) conserved the name *Bolitochara* (as separate from the genus *Zyras* Stephens) by fixing the type species as *Bolitochara lunulata* (Paykull). In the analysis, *B. lunulata* forms a monophyletic group with *B. lucida*, *B. (=Ditropalia) obliqua*, *B. (=Ditropalia) mulsanti*, and *B. (=Ditropalia) bella*. The lineage including these five taxa is robustly indicated to be monophyletic (see discussion above) and cannot be divided into less comprehensive monophyletic genus-level taxa. Under this interpretation, *Bolitochara* includes the type species of the genus *Ditropalia* Casey.

Ditropalia Casey.—Casey (1906) proposed the name *Ditropalia* to include those European "Bolitochara" which have the head more strongly narrowed behind than North American species (but neck greater than 1/2 as wide as head), and have a complete infraorbital carina. He included in this genus *Bolitochara bella* Maerkel (fixed as type species of *Ditropalia* by Fenyés 1918), *B. mulsanti* and *B. obliqua* as well as other undesignated European "Bolitochara" with similar features. Later Fenyés (1920), Moore, and Legner (1975) and others (see history

above) assigned North American bolitocharines to this genus. The analysis shows that those features on which *Ditropalia* was based are plesiotypic within the genus *Bolitochara* and the subtribe as a whole (see also discussion under *Bolitochara*). Even within *Bolitochara* the taxa assigned to *Ditropalia* do not form a monophyletic lineage. North American taxa previously assigned to *Ditropalia* do not form parts of monophyletic lineages which include the type species of *Ditropalia*. The conclusion that *Ditropalia* is a taxon based solely on plesiotypic features, and that other taxa have been assigned to it because of shared possession of plesiotypic features, cannot be avoided. For this reason I am placing the name *Ditropalia* Casey in junior synonymy with *Bolitochara* Mannerheim and recommending that it no longer be treated as a useful subgenus of *Bolitochara*.

Phymatura J. Sahlberg.—The genus *Phymatura* was originally described by J. Sahlberg (1876) to include the single European species *Bolitochara brevicollis* Kraatz. Casey (1906) subsequently designated the type of *Phymatura* to be *P. brevicollis* (Kraatz). It was originally distinguished from European *Bolitochara* because its members possess a much broader pronotum and head and shorter antenna with transverse antennomeres. Later Cameron (1939a) assigned a number of Oriental and Indian species to this *Phymatura*. In the cladistic analysis, *Phymatura brevicollis* forms a well-supported monophyletic group with two other representative species of *Phymatura* as well as the North American *Venusia blanchardi* (Casey). This group occurs on a different branch in the cladogram from *Bolitochara* and can be treated as a separate genus without ambiguity.

Phymaturosilusa Roubal.—The genus *Phymaturosilusa* was described by Roubal (1932) to include the single eastern European species *Phymaturosilusa magnifica* Roubal. It was characterized by relatively large size, very broad head and pronotum, and distinctive secondary sexual characteristics, including longer antennomeres of males in comparison to those of females. *Phymaturosilusa magnifica* appears on the cladogram in an unresolved trichotomy with two species of the North American taxon *Pleurotobia* Casey. *P. magnifica* is extremely similar to North American

Pleurotobia in external form and appearance, and differs primarily in having much smaller (virtually absent) lateral carinae on the male tergum VII and VIII. The monophyly of *Phymatosilusa* and *Pleurotobia* is robustly supported by synapomorphic features and there can be no reasonable doubt that they should be combined into one genus-level taxon. For this reason I am placing *Phymatosilusa* Roubal in junior synonymy with *Pleurotobia* Casey.

Pleurotobia Casey.—*Pleurotobia* was originally described by Casey (1906) to include three North American species. Fenyès (1918) subsequently designated *Pleurotobia suturalis* Casey as the type. Fenyès (1920) synonymized *Pleurotobia* with *Ditropalia* because of the possession of an intraorbital carina by members of both groups. This synonymy was perpetuated by Blackwelder (1952), Moore and Legner (1975) and other studies of the Bolitocharina. I have shown above that *Ditropalia* is based on plesiotypic characteristics and should not be used. In addition, the sampled members of *Pleurotobia* (+*Phymatosilusa*) form a well-supported monophyletic group which is the sister group to the European *Bolitochara*. None of the members of *Pleurotobia* unite with members of *Bolitochara*. Therefore, *Pleurotobia* is a valid genus-level taxon separate from *Bolitochara*. I will treat it as a genus. An alternative ranking would be to enlarge the concept of *Bolitochara* to include both monophyletic groups. *Bolitochara* would then still be monophyletic with two valid subgenera, *Bolitochara* (s. str.) and *Bolitochara* (*Pleurotobia*). However, members of *Pleurotobia* and *Bolitochara* are substantially different from each other in a variety of external structural features, as well as general appearance. Therefore, I can see little advantage in combining them into a single genus, and have chosen to treat them separately.

Pseudatheta Cameron.—*Pseudatheta* was described by Cameron (1920) to include the single species *Pseudatheta elegans* Cameron from Southeast Asia. Though he included the genus in the tribe Bolitocharini, he did not specifically assign it to the subtribe Bolitocharina. He subsequently described other species in this genus (1932, 1939a). The genus has not received subsequent study and

has always been treated as separate from *Bolitochara*. The ranking of *Pseudatheta* is problematic. The single species studied forms a monophyletic group with "*Sternotropa*" *zealandica* (see discussion below). However, the two taxa are dramatically different in external appearance as well as in apomorphic features. Furthermore, the apomorphies which unite them are not convincing (see analysis above). I, therefore, have elected to treat each as representing a valid genus-level taxon.

Silusida Casey.—*Silusida* was described by Casey (1906) to include two species of North American bolitocharines characterized by weakly rounded sides of the prothorax and short and strongly incrassate antennae with very transverse antennomeres IV–X. Fenyès (1918) later designated the type to be *Silusida marginella* (Casey). In contrast to the fate of most North American bolitocharine taxa [i.e., to be synonymized with *Bolitochara* (*Ditropalia*)], *Silusida* has most often been treated as a separate genus. However, Blackwelder (1952) indicated that it should be treated as a *Bolitochara*, and Seevers (1978) synonymized all North American bolitocharines with *Bolitochara*. However, the cladistic analysis indicates that *Silusida* is not closely related to *Bolitochara*. Furthermore, it does not combine into a monophyletic group with any other taxa examined in the analysis. Members of *Silusida* exhibit numerous apomorphic features which separate them from other bolitocharines. In spite of the low diversity of *Silusida* (a single valid known species—see taxonomic treatment), there is no phylogenetic justification for treating *Silusida* as a member of any other genus-level taxon. Therefore, I have chosen to maintain *Silusida* as a separate genus.

Stictalia Casey.—*Stictalia* was described by Casey (1906) to include a variety of North American bolitocharines which have the prothorax distinctly narrower than the elytra, the head slightly narrowed behind the eyes, and the mesocoxal cavities more narrowly separated by the meso- and metasternal processes than in other North American bolitocharines. This is the most diverse group of North American bolitocharines, with 17 species limited to the west coast of North America. Fenyès (1920) synonymized

Stictalia with *Ditropalia*, apparently because all members of *Stictalia* have a prominent and complete infraorbital carina. The cladistic analysis provides no evidence that the members of *Stictalia* are closely related to those of *Bolitochara*. The nine examined members of *Stictalia* combine into a monophyletic group, on a different branch of the cladogram than *Bolitochara* and substantially separated from it. Under the ranking criteria applied in this paper, the genus *Stictalia* clearly forms a valid genus-level taxon.

Venusia Casey.—The genus *Venusia* was described by Casey (1906) to include those North American bolitocharines which have a broad head, very broad and transverse prothorax, antennomeres which are elongate and do not gradually increase in width apically, and different secondary sexual characteristics. Fenyés (1918) subsequently fixed the type to be *Venusia picta* Casey (= *Bolitochara blanchardi* Casey). Fenyés (1920) synonymized *Venusia* with *Ditropalia*, apparently because members of *Venusia* possess a prominent and complete infraorbital ridge. This treatment has been followed by all subsequent workers. However, in the cladistic analysis, the single valid species of *Venusia* examined combines as a part of a monophyletic group with all members of *Phymatura* represented in the analysis. This combination is robustly supported by numerous synapomorphies (see cladistic analysis). The similarity of the aedeagus of members of *Venusia* and *Phymatura* is especially striking and quite different from the form of the aedeagus of any other group of bolitocharines. The primary difference between members of *Venusia* and *Phymatura* is found in the elongate antennomeres and non-incrassate antenna of members of *Venusia* (transverse antennomeres and incrassate antenna for most members of *Phymatura*) and the more prominent carina on tergum VII of males of *Venusia*. These differences are overshadowed by the synapomorphies that the two groups share. The phylogenetic evidence provides strong support for the conclusion that *Phymatura* and *Venusia* represent a single genus-level taxon. I therefore am placing *Venusia* Casey in junior synonymy with *Phymatura* Sahlberg.

"*Bolitochara*" n. sp. A (= *Hongophila* new

genus).—This taxon was designated as a "*Bolitochara*" solely to provide a name for discussion. *Bolitochara* n. sp. A is known only from the mountain systems of the southwestern United States; however, I have seen specimens of several closely related species from Mexico. In the cladistic analysis this taxon is shown to be the basal member of the branch which includes *Pleurotobia* and *Bolitochara*. However, it shares few synapomorphies with either of these taxa. In addition, the aedeagus, spermathecae and secondary sexual characteristics of members of "*Bolitochara*" n. sp. A are built on dramatically different, and highly derived patterns. If *Bolitochara* and *Pleurotobia* are treated as separate genera then there is no choice but to treat "*Bolitochara*" n. sp. A as a new genus level taxon. Because members of "*Bolitochara*" n. sp. A are relatively plesiotypic in external features, the genus is relatively difficult to characterize and recognize, based on apomorphic features, without examination of sexual characteristics. "*Bolitochara*" n. sp. A could only be incorporated into a previously described genus by expanding the concept of *Bolitochara* to include all members of the "*Bolitochara*" lineage (*Bolitochara* + *Pleurotobia* + "*Bolitochara*" n. sp. A). While this would reduce the number of genera, it would have the effect of making *Bolitochara* a structurally very diverse taxon and subsequently, it would be very difficult to characterize or distinguish from genus-level taxa on the "*Stictalia*" lineage. Such a ranking decision would also have the effect of requiring that all taxa on the "*Stictalia*" lineage also be treated as a single genus-level taxon (since the "*Bolitochara*" and "*Stictalia*" lineages are sister taxa and therefore coordinate taxa). This, in my opinion, would result in more taxonomic problems and difficult to define taxa than would the alternative ranking which requires a new genus-level taxon for "*Bolitochara*" n. sp. A. I, therefore, have chosen to treat "*Bolitochara*" n. sp. A as a new genus-level taxon (see Taxonomic Treatment, *Hongophila* new genus).

"*Bolitochara*" n. sp. B (= *Neotobia* new genus).—As above, the name "*Bolitochara*" n. sp. B was chosen only to provide a label for discussion. Only a single undescribed species of this taxon is known from widely

scattered localities across the northern part of North America from the Canadian Rockies to the northeastern United States. "*Bolitochara*" n. sp. B forms a weakly supported monophyletic lineage with members of *Phymatura* and *Venusia* in some analyses (Figs. 2, 5). However, "*Bolitochara*" n. sp. B is sister group to a diversity of taxa in other analyses (Figs. 3, 4). Two alternative rankings of "*Bolitochara*" n. sp. B are possible. One could enlarge *Phymatura* to encompass "*Bolitochara*" n. sp. B. This would result in a broad genus *Phymatura* which would be difficult to characterize or recognize, and it would destroy the striking uniformity within *Phymatura* of highly distinctive and apomorphic aedeagal structures exhibited by members of *Phymatura* and *Venusia*. The alternative is to treat "*Bolitochara*" n. sp. B as a new genus-level taxon (see Taxonomic Treatment, *Neotobia* new genus). This latter choice seems to me to be the better one since then each taxon can be recognized and characterized based on apomorphic features. Also, "*Bolitochara*" n. sp. B does not group as part of a monophyletic group with *Phymatura* in two of the alternative phylogenies (see Figs. 3, 4). This results in some doubt about the correct placement of the two lineages as sister groups. Therefore including them together in one genus is questionable.

"*Sternotropa*" *zealandica* Cameron (= *Austrasilida* new genus).—The name *Sternotropa zealandica* was applied by Cameron (1947) to a small "bolitocharine" found in New Zealand. However, it is not closely related to other members of *Sternotropa*, a genus in the subtribe Gyrophaenina (Ashe, 1984), and is clearly not a gyrophaenine. However, though externally similar to many Bolitocharina, its inclusion in the subtribe is problematic. For reasons discussed elsewhere I have tentatively accepted it as a bolitocharine (see discussion under "Choice of Taxa"). In the cladistic analysis "*Sternotropa*" *zealandica* appears as sister group to *Pseudatheta elegans* (see discussion under *Pseudatheta* above). However, the monophyly of the lineage that includes these two taxa is very weakly supported (see "Cladistic Analysis" section for discussion). The problem seems to center on the unusual combination of characteristics exhibited by "*Sternotropa*"

zealandica. Many of these are aberrant for the Bolitocharina as a whole. This makes "S." *zealandica* difficult to fit on the tree, and results in a considerable increase in homoplasy when it is included in the analysis. The position of "S." *zealandica* (as sister group to *Pseudatheta*) is too weakly supported to base any taxonomic decisions on such a placement. Changes in character coding, addition of only a small number of characters, or addition of other taxa could very easily alter such a tentative placement. With these considerations it seems that the only reasonable action is to treat "*Sternotropa*" *zealandica* as a new genus-level taxon. Under any circumstances, the taxon needs a new generic assignment, since it is clearly not a member of *Sternotropa* (see Taxonomic Treatment, *Austrasilida* new genus).

TAXONOMIC TREATMENT

SUBTRIBE BOLITOCHARINA

Diagnosis.—Adults of the Subtribe Bolitocharina can be recognized by the combination of 4,4,5 tarsal segmentation; 3-articled, nonstyliform labial palpi (Figs. 5, 13, 34, 55); mandibles with large patch of densely arranged denticles in molar area of ventral (abcondylar) side (Figs. 10, 31, 52); ligula of labium elongate and bifid at apex; medial setae of prementum either one laterally behind the other or one directly behind the other (Fig. 34); medial pseudopore field of prementum very narrow and without pseudopores (Fig. 13); lacinia of maxilla with numerous spines and setae on apical 0.75 of inner face (Figs. 11, 32); many with mesocoxae moderately broadly separated by broad meso- and metasternal processes; and many with male secondary sexual characters consisting of medial or lateral carinae or knob on terga VII and VIII, and broadly emarginate margin of tergum VIII with 3 to 5 small to moderate-sized denticles in each half of emargination.

Description.—Body length 1.2–4.2 mm. Body form various (Figs. 6, 27, 48, 80, 95), most elongate and more or less parallel-sided. Body color various, most with contrasting light and dark colors, especially on elytra.

Head.—Distinctly broader than long to distinctly elongate. Infraorbital carina strongly developed and complete to reduced and present only faintly near mandibular insertion. Neck absent (Fig. 81) to slightly developed (Fig. 22) or well developed (Fig. 7), prominent, less than 1/2 width of head. Eye size relatively large, length greater than 1.5 times length of tempora, to small, length less than 1.0 times length of tempora. Head setation directed medially and anteriorly or all setae directed anteriorly or all directed medially.

Mouthparts.—Labrum (Figs. 8, 29, 50) with major setae well developed, without accessory setae; medial sensilla well developed; lateral sensillum row with 3 to 5 sensilla, sensilla more or less distant from lateral margin. Maxillary palpus 4-articled. Lacinia (Figs. 12, 33, 54) with single to multiple rows of teeth in apical 0.25, with numerous spines and setae on apical 0.75 of inner face. Galea with numerous close rows of setae apically. Mandibles (Figs. 10, 31, 52) more or less robust, apices simple; right with well-developed preapical tooth; ventral molar area with large patch of densely arranged and well-developed denticles; prostheca well developed, with flattened and apically bifid structures in basal 0.5. Labial palpus distinctly 3-articled, not styliform. Ligula (Figs. 13, 34, 55) of labium elongate, bifid apically. Medial setae of labium two, bases arranged one behind the other, setal bases either laterally behind each other or in same antero-posterior line. Medial pseudopore field very narrow, without pseudopores; lateral pore field with one spinose pore, two real pores and most with numerous pseudopores.

Thorax.—Pronotum transverse to more or less quadrate; posterior margin moderately bisinuate to broadly rounded. Pronotum almost as wide as base of elytra to distinctly narrower than base of elytra. Hypomera broadly visible in lateral aspect. Elytral apical angles markedly to moderately sinuate. Mesosternum with medial carina markedly developed (Fig. 154) and complete to apex of mesosternal process or well developed only basally (Fig. 123). Mesosternal process broad or narrow, extended between coxae 0.5 or greater length of coxae to contact or virtually contact rounded metasternal process, isthmus very short or absent; mesocoxae moderately to narrowly separated. Tarsal segmentation 4,4,5.

Abdomen.—Abdominal terga III-V or III-VI more or less deeply transversely impressed. Tergum VII with abdominal gland openings on anterior margin.

Male Secondary Sexual Characteristics.—Most with moderately developed to strong carina or knob medially on terga VII and VIII (Fig. 18), or two or three oblique carinae on each side (Fig. 60), greatly reduced to small knob and scattered asperities in some (Fig. 105) to absent in a few. Some with small knob or distinct carina at sutural margin of elytra. Most with apical margin of tergum VIII broadly emarginate with row of small to moderate-sized denticles in emargination (Figs. 18, 39), emargination and denticles greatly reduced in some (Fig. 111). Sternum VIII triangularly produced into a distinct lobe posteriorly.

Aedeagus.—Median lobe and parameres varied. Flagellum long or short, tubular, moderately sclerotized. Median lobe with internal structure of pair of sclerotized plates (Figs. 21, 62, 128) or such plates absent (Figs. 41, 93, 107, 146). Apical process simple and tentlike (Figs. 21, 62) or spinose (Figs. 41, 46) or recurved structures

(Figs. 107, 112, 114). Paramere with apical lobe very long, length greater than 0.5 times length of basal portion in most (Fig. 61), shorter in some (Fig. 145).

Female Genitalia.—Spermathecal tube membranous to slightly sclerotized, short to very long and convoluted or complexly looped, without lateral flangelike plate (except in *Austrasilida* new genus). Spermatheca simple, basal bulb elongate (Fig. 131), rounded (Fig. 24), or slightly knobbed basally (Fig. 109); neck more or less straight (Fig. 94) to bent 90° or more (Figs. 109, 131).

Discussion and Reclassification.—The subtribe Bolitocharina as here defined is comprised of a number of genera that share several apomorphic features as listed above (see Choice of Taxa and Cladistic Analysis). Treated in this way, the subtribe Bolitocharina is more narrow than its treatment in such works as Lohse (1974) and SeEVERS (1978) in that it does not include *Leptusa* and its relatives. *Leptusa* and similar genera [essentially the "Group Leptusae" of Fenyés (1918)] lack these apomorphies. In addition, this latter group of genera has 2-articled labial palpi (3-articled in the Bolitocharina), an undivided, elongate ligula of the labium (divided in the Bolitocharina), and a very different lacinia of the maxilla. These genera should be placed in a separate subtribe centered on *Leptusa*, though the generic composition of this subtribe is not yet clear and requires additional study.

Restricting the subtribe Bolitocharina to be comprised of those genera sharing the synapomorphies listed above serves to make the group much more homogeneous in both external features and in biology. Both larvae and adults of all taxa are associated with macroscopic fruiting bodies of fungi, especially members of the Polyporaceae and some ligniferous Agaricales. This uniformity of habitat preferences may be an additional synapomorphy linking members of the Bolitocharina. The concordance among the three synapomorphies listed and the habitat preference provides relatively robust evidence that the subtribe so defined is monophyletic.

In this revision I recognize nine genera in the subtribe. These are:

Bolitochara Mannerheim

Ditropalia Casey

Phymatura J. Sahlberg

Venusia Casey

Pleurotobia Casey

Phymaturosilusa Roubal

Pseudatheta Cameron

Silusida Casey

Stictalia Casey

Hongophila new genus (for "*Bolitochara*" n. sp. A)

Neotobia new genus (for "*Bolitochara*" n. sp. B)

Austrasilida new genus (for *Sternotropa zealandica* Cameron)

Justification for dividing available taxa into these genera is provided in the phylogenetic section of this paper.

IDENTIFICATION

One of the consequences of the classification philosophy adopted in this study is that, while many bolitocharine genus-level taxa are easily distinguished, others are difficult to identify based on easily observable external characteristics. Some can only be identified with certainty by examination of microscopic features of the mouthparts, or by examination of male secondary sexual or aedeagal characteristics. This problem is illustrated by problems with separating specimens of *Hongophila* and *Neotobia*. Because of retention of many primitive features in members of both of these taxa, they are surprisingly similar in external appearance. However, they are not closely related within the Bolitocharina. Differences in male secondary sexual features provide the most readily accessible means for distinguishing them. But they can also be distinguished by other features which can only be observed with compound optics.

A similar problem results from considering the taxa from a worldwide perspective. Many taxa which are distinct when faunas are considered locally have broader variation in the world fauna such that taxa that are not very closely related have some members which are similar in many external features. This is illustrated by the example of *Phymatura*. When only Old World *Phymatura* are considered, the genus can be easily characterized based on readily observable external features. However, when the North American *Phymatura* (= *Venusia*) *blanchardi* (Casey) is included in the genus, many of the previously useful key characteristics, especially in the antennae, are no longer distinctive for the group. However, there can be no doubt that they represent a mono-

phyletic genus-level taxon based on the highly derived and unique aedeagal structure.

Many of the problems associated with identification of genera among bolitocharines, and the Aleocharinae as a whole, are a result of the fact that specimens of these taxa are small, often minute. As a result many very useful identification characteristics can only be observed by examination of properly prepared and dissected specimens using compound optics. This is unfortunate, but is probably unavoidable in this group. Reluctance to study specimens of the Aleocharinae in this way has been one of the reasons for the present taxonomic difficulty of the group.

With the above considerations in mind, I have tried to provide a key to the genera of the Bolitocharina using characteristics that are as readily observable as possible. I have placed more easily observable characteristics at the beginning of each couplet, and those which are more difficult to observe, require special preparation and handling, or are limited to one sex, toward the end of the couplet. This arrangement does not necessarily reflect the reliability of the characters. Often those which are most difficult to observe are the most reliable for correct identification.

The key below will provide correct identification of specimens of all the taxa that I have had opportunity to examine. I have been unable to obtain specimens of some taxa (see descriptive section). Examination of these, as well as bolitocharine taxa that are likely to be discovered in the future, may require modification of the key. Nonetheless, I hope that this key will provide access to the bolitocharine fauna of the world, and will lead to studies which will result in its subsequent revision.

KEY TO KNOWN GENERA OF THE SUBTRIBE BOLITOCHARINA OF THE WORLD

1. Pronotum broadly transverse, 1.35–1.50 (most 1.4–1.5) times as wide as long (Figs. 27, 48, 80, 115). Pronotal base of most slightly to moderately bisinuate (not bisinuate on specimens of *Neotobia* but then base of pronotum as wide as elytra). Base of pronotum as wide as, or virtually as wide as, base of elytra, not appearing noticeably narrower than elytra. Eyes large, length of most greater than 1.2 times length of temple (Figs. 28, 49, 68, 81, 132, 147) [eye length of *Hongophila* 1.1–1.2 times length of temples (Fig. 116) but then pronotum 1.4 times as wide as long and base of pronotum as wide as base of elytra] 3
- . Pronotum less broadly transverse, 1.1–1.3 times as wide as long (Figs. 5, 95, 110). Pronotal base broadly rounded, not bisinuate. Base of pronotum slightly to moderately narrower than base of elytra. Eyes small, length of most less than 1.1 times length of temple (Figs. 7, 22, 95) (eyes of *Stictalia nigrina* and *Bolitochara obliqua* 1.1–1.2 times length of temple, but other features apply) 2
2. Head moderately to strongly narrowed behind eyes to form distinct neck (Figs. 7, 22). Mesocoxal cavities moderately broadly separated by intercoxal processes, apex of mesosternal process rounded to more or less truncate (Fig. 14). Male sternum VI with small asetose medial lobe on posterior margin (Figs. 16, 17), sternum VII with concentration of setose glandular pores medially in addition to broad band of sensory pores basally (Figs. 16, 17). Posterior angular projection of male sternum VIII without asetose posterior margin (Fig. 17). Median lobe of aedeagus with pair of distinct sclerotized internal plates (Figs. 21, 26). Spermathecal duct not sclerotized and complexly looped (Figs. 19, 24). Most taxa known from Old World *Bolitochara*

- Head at most only slightly narrowed behind eyes to indistinct neck (Fig. 96). Mesocoxal cavities narrowly to very narrowly separated by intercoxal processes, apex of mesosternal process sharply pointed (Fig. 103). Male sternum VI without small medial lobe on posterior margin, sternum VII with broad band of sensory pores basally, without concentration of setose glandular pores medially (Fig. 106). Posterior angular projection of male sternum VIII with asetose posterior margin (Fig. 106). Median lobe of aedeagus without distinct pair of internal sclerotized plates (Figs. 107, 112, 114). Spermathecal duct sclerotized and complexly looped (Fig. 109). Known only from west coast of North America *Stictalia*
- 3. Pronotal hypomeron strongly horizontally inflexed throughout, only narrowly visible, or not visible, in lateral aspect 4
 - Pronotal hypomeron inflexed basally in some but deflexed toward vertical anteriorly, at least anterior half broadly visible in lateral aspect 7
- 4. Size larger, length 2.1–4.0 mm. Abdominal terga III–V with moderate transverse basal impressions. Wings with 2 to 5 setose projections on flabellum (Figs. 36, 89). Triangular projection of male sternum VIII with distinct asetose posterior margin occupying at least 50 percent of width of posterior margin (Figs. 38, 90) 5
 - Size smaller, length 1.5–2.0 mm. Abdominal terga III–IV with at most moderate to slight basal impressions. Wings without setose projections on flabellum. Triangular projection of male sternum VIII without asetose margin or asetose area very small, indistinct and limited only to apex of projection (Figs. 86, 155) 6
- 5. Postero-lateral angles of pronotum moderately to sharply angulate (Fig. 27). Mesocoxal cavities moderately broadly separated by intercoxal processes, mesosternal process broader, apex not acutely pointed (Fig. 35). Median lobe of aedeagus distinctive, apical process elongate, slender; flagellum moderately elongate, slender and acutely pointed (Figs. 41, 46). Known from Europe, India, Asia, Southeast Asia, Japan, and eastern North America *Phymatura*
 - Postero-lateral angles of pronotum broadly rounded (Fig. 80). Mesocoxal cavities narrowly separated by intercoxal processes, mesosternal process narrow, apex acutely pointed (Fig. 88). Median lobe of aedeagus distinctive, apical process large, tentlike; flagellum short, tubular and obliquely truncate apically (Fig. 93). Known only from eastern North America *Silusida*
- 6. Mesocoxal cavities narrowly separated by intercoxal processes; mesosternal process narrow, pointed apically (Fig. 75). Mesosternum without medial longitudinal carina (Fig. 75). Head setae mostly directed medially. Lacinia of maxilla with single row of teeth on apical third (Figs. 71, 72). Ligula of labium long, bifid only in apical third (Fig. 74). Known from India, Southeast Asia, Nepal, Africa. *Pseudatheta*
 - Mesocoxal cavities widely separated by intercoxal processes; mesosternal process broad, broadly rounded apically (Fig. 154). Mesosternum with strong medial longitudinal carina (Fig. 154). Head setae mostly directed anteriorly. Lacinia of maxilla with patch of numerous spines forming a dense “brush” on apical third (Figs. 150, 151). Ligula of labium short, split to the base into two widely separated lobes (Fig. 153). Known only from New Zealand *Austrasilida zealandica*
- 7. Eyes very large, eye length 1.3–1.5 times length of temple (Fig. 149). Mesocoxal cavities very widely separated by intercoxal cavities; mesosternal process broad, broadly rounded apically (Fig. 56). Mesosternal medial carina extended 0.60–0.75 times combined length of mesosternum and mesosternal process (Fig. 56). Wing with 10 to 13 setose projections on flabellum (Fig. 57). Lacinia of maxilla with 3 to 4 irregular rows of teeth on apical quarter (Fig. 54). Male tergum VII with oblique to posteriorly directed carinae on each side of midline (variously developed on different males, reduced or absent on some) (Figs. 60, 64); male tergum VIII with large medial carina and 1 to 2 smaller lateral carinae on each side (Figs. 60, 64). Median lobe of aedeagus with large, tentlike apical process, and internal sac with pair of large sclerotized platelike structures (Figs. 62, 66). Known from eastern North America and central Europe *Pleurotobia*
 - Eyes moderately large, eye length 1.1–1.3 times length of temple (Figs. 116, 132). Mesocoxal cavities moderately to narrowly separated by intercoxal processes, mesosternal process narrow, slightly to sharply pointed apically (Figs. 123, 139). Mesosternal medial carina extended only 0.2–0.4 times combined length of mesosternum and mesosternal process (Figs. 123, 139). Wings with 3 to 8 setose projections on flabellum (Figs. 124, 140). Lacinia of maxilla with 1 row of teeth on apical quarter (Figs. 121, 137). Male tergum VII either with small medial tubercle and larger lateral tubercles (Fig. 127) or moderate medial tubercle (Fig.

- 144); male tergum VIII either with numerous small asperities (Fig. 127) or small medial tubercle (Fig. 144). Medial lobe of aedeagus with elongate slender (Fig. 128) or bilid (Fig. 146) apical lobe, and internal sac either without sclerotized plates or sclerotized structures spinose rather than platelike 8
8. Antenna with at least some of articles 5 to 10 distinctly elongate. Wings with 6 to 8 setose lobes on flabellum (Fig. 140). Male sternum VI without medial projecting lobe on posterior margin. Male sternum VII with broad band of numerous sensory pores basally, without medial concentration of setose sensory pores (Fig. 141). Posterior triangular projection of male sternum VIII with distinct asetose posterior margin (Fig. 141). Known only from the northern half of North America *Neotobia*
- Antenna with articles 5 to 10 either quadrate or transverse. Wings with 3 to 5 (a few specimens with 6) setose lobes on flabellum (Fig. 124). Male sternum VI with small medial projecting lobe on posterior margin (Figs. 125, 126). Male sternum VII with medial concentration of setose sensory pores as well as broad band of sensory pores basally (Figs. 125, 126). Posterior projection of male sternum VIII without distinct asetose posterior margin (Fig. 125). Known only from the southwestern United States and Mexico *Hongophila*

Genus *Bolitochara* Mannerheim
(Figs. 6-26)

Bolitochara Mannerheim 1831, p. 489. Type species *Bolitochara lunulata* (Paykull). Fixed by International Commission of Zoological Nomenclature (1961, Opinion 599); not *Bolitochara collaris* (Paykull) as proposed by Blackwelder 1952.—Mannerheim 1831: 489.—Stephens 1832: 431.—Erichson 1837: 296.—Kraatz 1858: 36.—Thomson 1860: 272.—Mulsant and Rey 1871: 194.—Ganglbauer 1895: 262.—Casey 1906: 263.—Fenyés 1920: 111-112.—Lohse 1974: 62.—Scheerpeltz and Höfler 1948: 178.—Seevers 1978: 164.

Ditropalia Casey 1906, p. 263. Type species *Ditropalia bella* (Maerkel). Fixed by Fenyés 1918, p. 22.—Casey 1906: 263.—Fenyés 1920: 114.—Seevers 1978: 164.

Diagnosis.—Among bolitocharine genera specimens of *Bolitochara* can be easily recognized by the combination of: relatively large size, adults 3.0-5.0 mm in length; relatively small eyes, 1.1-0.8 times length of temple; head slightly to moderately narrowed behind the eyes to form a slight to very distinct neck (Figs. 7, 22); relatively narrow pronotum (Fig. 6), 1.1-1.2 times as wide as long with fully exposed hypomerion in lateral aspect; pronotum distinctly narrower than base of elytra, not bisinuate basally; moderately widely separated mesocoxal cavities, apex of mesosternal process rounded to more or less truncate (Fig. 14); terga III-V^r or III-VI with moderate to deep transverse basal impressions; sterna III-V with moderate transverse basal impressions; male sternum VI with medial lobate asetose projection on posterior margin (Fig. 17); male sternum VII with concentration of setose pores medially, as well as band of numerous sensory pores basally (Fig. 16); triangular projection of male sternum VIII without asetose posterior margin (Fig. 16); median lobe of aedeagus with large, tentlike apical process, two platelike structures on internal sac, and tubelike flagellum (Fig. 21). This is the only bolitocharine genus which includes some members which lack a complete infraorbital carina on the head.

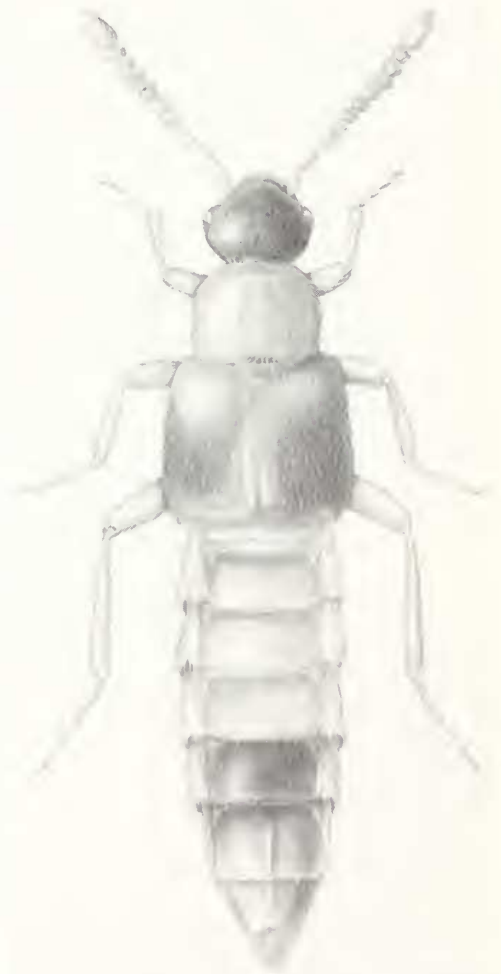
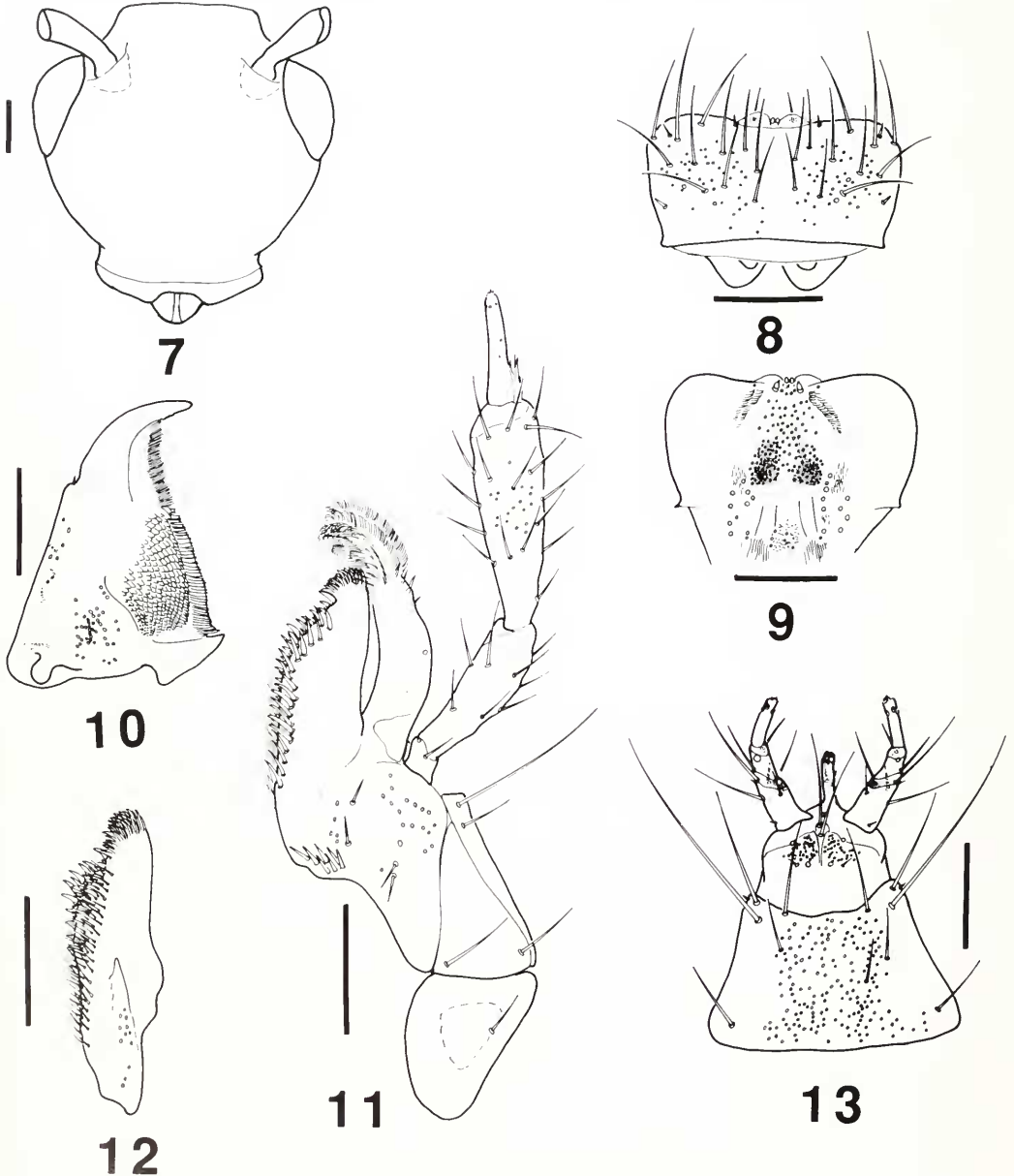


Fig. 6. *Bolitochara lunulata* Payk. Habitus. Total length = 4.2 mm.

Description (Fig. 6).—Lengths of adults 3.0–5.0 mm. Body elongate, more or less parallel-sided and convex in cross section. Surface sculpture faint to absent, surface shiny. Body slightly to moderately pubescent; microsetae stiff, moderately dense to widely dispersed; punctures small and inconspicuous to large and prominent, asperate or not. Macrosetae inconspicuous.

Head (Fig. 7).—More or less oval to slightly elongate, rounded and narrowed behind the eyes to form conspicuous neck less than 0.5 times width of head, to inconspicuously narrowed behind to form, at most, a slight neck (Fig. 22). Sculpture absent, integument shiny. Punctures moderately large, shallow, distant to small and inconspicuous; setae fine to moderately stiff, di-

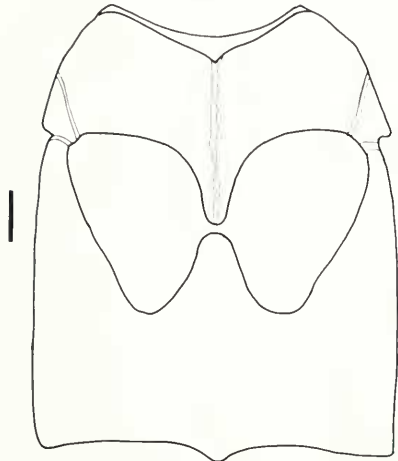


Figs. 7–13. *Bolitochara lunulata* Payk. 7, Head, dorsal aspect. 8, Labrum, dorsal aspect. 9, Labrum, epipharyngeal aspect. 10, Mandible, ventral aspect. 11, Maxilla, ventral aspect. 12, Lacina of maxilla, dorsal aspect. 13, Labium, ventral aspect. (Scale line = 0.1 mm.)

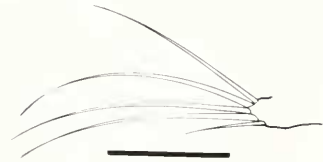
rected medially and anteriorly or only medially. Eyes moderate sized to small, 1.1–0.8 times length of temple. Infraorbital carina moderately developed and complete, or absent except faintly near maxillary insertion. Antenna moderately long to elongate, not incrassate toward apex; article 4 quadrate to elongate, similar to 5 to 10 in setation and sculpture; article 5 transverse to elongate; article 10 transverse to quadrate, anten-

nal articles 5 to 10 decreasing in relative lengths apically.

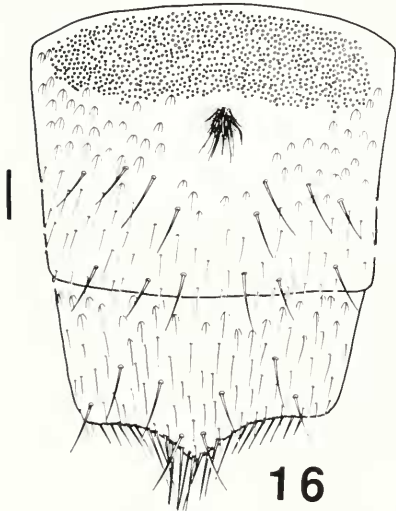
Mouthparts.—Labrum (Figs. 8, 9) with epipharyngeal area with medial pores moderately large to large, numerous, in a well-delimited longitudinal field. Mandibles with abcondylar molar patch of denticles large, denticles numerous and close (Fig. 10). Maxilla with teeth on apical 0.25 of lacinia various, from numerous, in



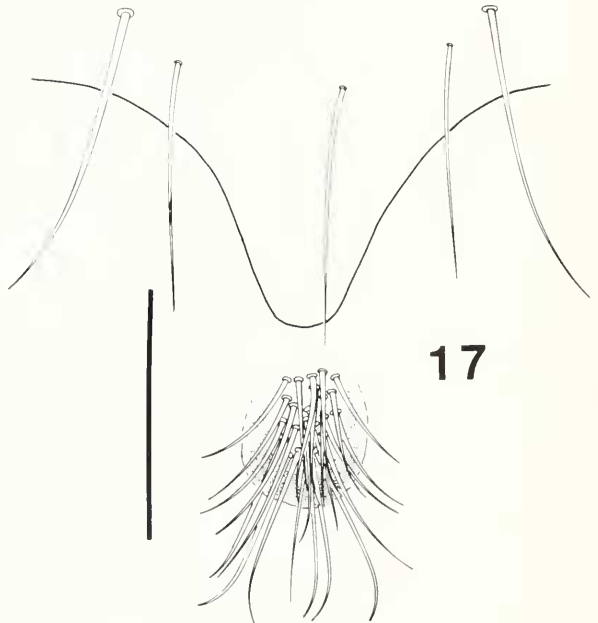
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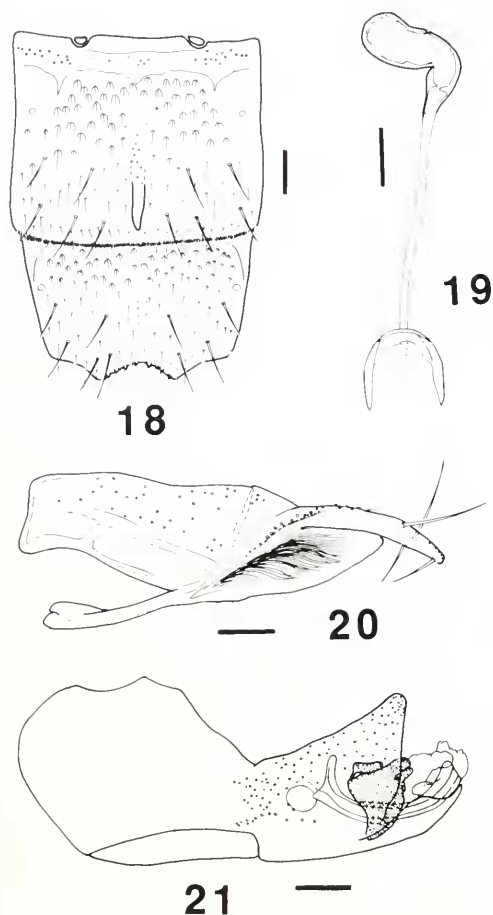


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Figs. 14–17. *Bolitochara lunulata* Payk. 14, Meso-metasternum, ventral aspect. 15, Flabellum of wing. 16, Male sternal features, posterior margin of sternum VI, and sternum VII and VIII. 17, Male, detail of asetose lobe of sternum VI and concentration of setose pores on sternum VII. (Scale line = 0.1 mm.)



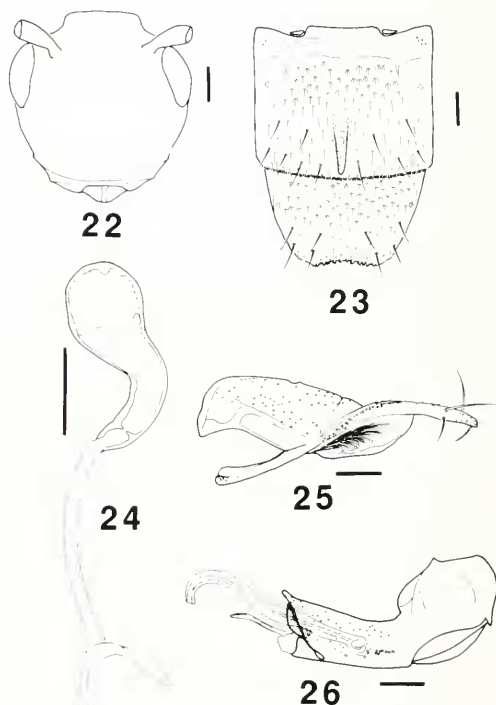
Figs. 18-21. *Bolitochara lunulata* Payk. 18, Male terga VII and VIII. 19, Female, spermatheca. 20, Male, paramere of aedeagus, external aspect. 21, Male, median lobe of aedeagus, lateral aspect. (Scale line = 0.1 mm.)

several irregular rows forming a dense patch of teeth (Fig. 12), to fewer, in only a single row; galeal apex with 8 to 10 rows of unmodified (setose) setae or modified subspatulate or flattened setae (Fig. 11). Labium (Fig. 13) typical of subtribe, with pair of sensory setae on ligula, sensory setae moderate sized or small; two medial setae of labium present, bases arranged one laterally behind the other or one directly behind the other, setal insertions close to distant; medial pseudopore field narrow, without pseudopores.

Thorax.—Pronotum relatively narrow, 1.1-1.2 times as wide as long, slightly to moderately convex in dorsal outline; distinctly narrower at base than base of elytra; postero-lateral angles slightly to strongly angulate; base not bisinuate; punctures large to small, numerous, dense, microsetae fine, moderately dense; integument

strongly shiny, without microsculpture. Elytra with postero-lateral angles moderately sinuate; punctures large, lunulate (open behind), very close to moderately so; microsetae fine, moderately dense. Wings with 3 to 8 (most with 5 to 8) setose lobes on moderately developed flabellum (Fig. 15). Hypomeron broadly visible in lateral aspect, deflexed to near vertical throughout, anterior margin of hypomeron contacting lateral line of pronotum distinctly posterior to antero-lateral angles. Mesosternal carina present, complete to apex of process or fading medially. Mesocoxal cavities moderately to broadly separated by meso- and metasternal processes (Fig. 14); relative lengths mesosternal : isthmus : metasternal process varies from 4 : 0 : 3 to 7 : 1 : 5; apex of mesosternal process rounded, apex of metasternal process subtruncate to broadly rounded. Hind tarsomere I almost to fully as long as II and III together (0.7-1.0 times as long as II and III).

Abdomen.—More or less parallel-sided; terga III-V or III-VI with deep transverse basal impressions; punctures moderately large, lunulate, distant to close; microsetae fine and distant to moderately dense, all microsetae on basal terga directed posteriorly; macrosetae inconspicuous.



Figs. 22-26. *Bolitochara bella* (Maerkel). 22, Head, dorsal aspect. 23, Male, terga VII-VIII. 24, Female, spermatheca. 25, Male, paramere, external aspect. 26, Male, median lobe of aedeagus, lateral aspect. (Scale line = 0.1 mm.)

Sterna III-V with moderate transverse basal impressions.

Secondary Sexual Characteristics.—Males: each elytron with moderate to small carina near suture in posterior 0.5–0.2 (most species) to elytra without carinae (a few species); tergum VII of most (Figs. 18, 23) with moderate to strong medial carina 0.5–0.6 times length of tergum, some with additional carinate asperities on each side of carina, or medial carina absent from tergum VII and surface with small scattered asperities; tergum VIII (Figs. 18, 23) broadly emarginate posteriorly, with 4 to 6 denticles in emargination on each side of midline, denticles moderate in size to minute and faint, virtually absent in some; tergum VIII with long medial carina or carina absent and a few faint scattered asperities present or without asperities; sternum VI (Figs. 16, 17) with small medial lobe on posterior margin, medial lobe asetose; sternum VII with concentration of setose glandular pores medially, porose area large, as well as broad band of sensory pores basally (Figs. 16, 17); sternum VIII with posterior triangular projection, projection without asetose posterior margin (Fig. 16).

Aedeagus.—Paramere (Figs. 20, 25) with apical lobe of paramerite relatively short (<0.5 times length of paramerite) to long (0.8–1.0 times length of paramerite); setae 1 to 4 of apical lobe of paramerite long, not clustered near tip. Aedeagus (Figs. 21, 26) with apical lobe large, tentlike; internal sac with pair of large sclerotized platelike structures; flagellum short, tubular.

Spermatheca (Figs. 19, 24).—Basal bulb simple, apex rounded; spermathecal tube membranous, more or less straight; neck bent $\leq 90^\circ$ angle. Vaginal sclerotization moderate, about 0.5–0.7 of complete circle of sclerotized cuticle.

Discussion.—About 30 species have been described in either *Ditropalia* or *Bolitochara* (not including those transferred to *Ditropalia* but more correctly placed in other genera). A complete study of all taxa is outside the range of this study. However, in addition to the five Palearctic taxa included in the phylogenetic analysis (Appendix 2), I have examined the following five other Palearctic taxa: *Bolitochara humeralis* (Lucas) (from *Ditropalia*); *B. laufferi* Bernhauer (from *Ditropalia*); *B. reyi* Sharp; *B. schusteri* Bernhauer (from *Ditropalia*); and *B. varia* Erichson (from *Ditropalia*). All of these are correctly placed in *Bolitochara* as here defined.

Other species, that I have not examined, have been described from southeast Asia [*Ditropalia strigosa* Cameron, *D. granulata* Cameron, *D. nigra* Cameron, *Bolitochara (Ditropalia) smetanai* Pace], and Japan (*B. varipes* Sharp, *B. iridescens* Sawada, *Ditropalia lobata* Sawada) as well as others from the Palearctic. In addition, there are a number of species of doubtful placement described from Chili, Columbia, Australia, New Guinea, and Argentina (see Fenyes, 1918–1921 for list). It is interesting that no species which can be placed in

Bolitochara as here defined has been found in North America.

Genus *Phymatura* J. Sahlberg
(Figs. 27–47)

Phymatura J. Sahlberg 1876, p. 85. Type species *Phymatura brevicollis* (Kraatz.). Fixed by Casey 1906, p. 264.—J. Sahlberg 1876: 85.—Ganglbauer 1895: 266.—Casey 1906: 264.—Fenyes 1920: 116.—Cameron 1939a: 217.—Lohse 1974: 61.

Venusia Casey 1906, p. 272. Type species *Venusia picta* Casey. Fixed by Fenyes 1920, p. 26.—Casey 1906: 272.—Fenyes 1920: 114 (as a synonym of *Ditropalia* Casey).—Seevers 1978: 164 (as a synonym of *Bolitochara* Mannerheim).

Diagnosis.—Members of *Phymatura* can be recognized by the following combination of characteristics: eyes large, about 1.2–2.0 times as long as temples; head not noticeably narrowed behind

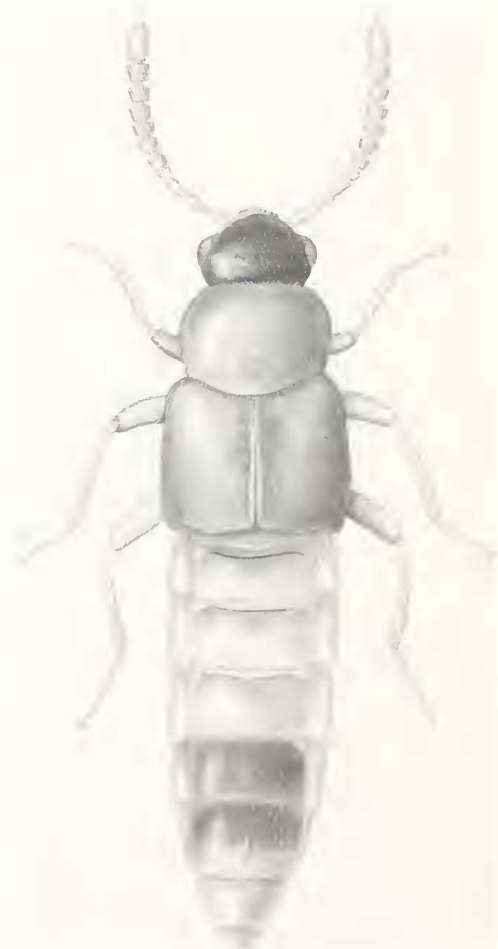
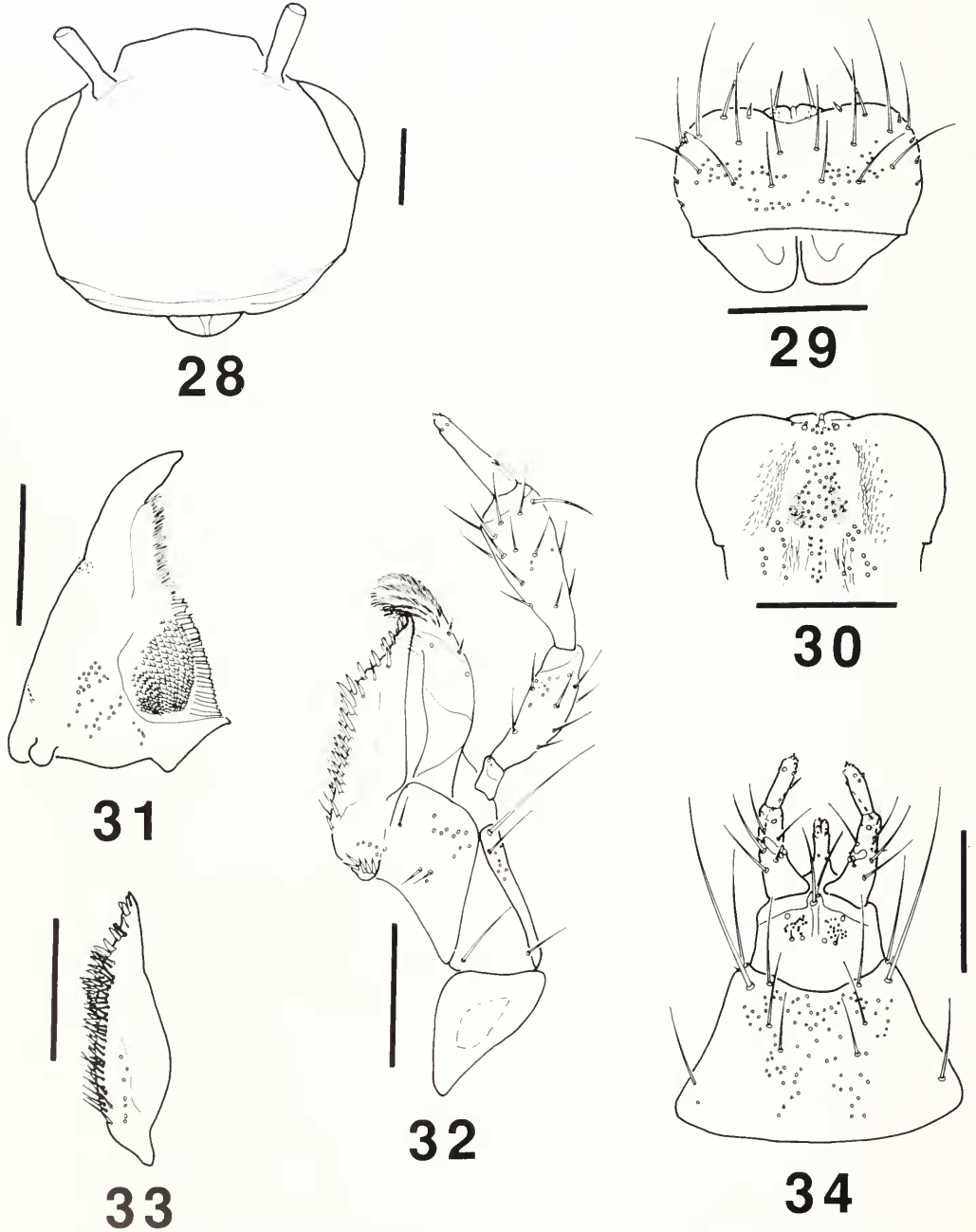


Fig. 27. *Phymatura* (= *Venusia*) *blanchardi* (Casey). Habitus. Length = 3.1 mm.

eyes to form a neck; pronotum strongly transverse, 1.4-1.5 times as wide as long; pronotum as wide as, or virtually as wide as, base of elytra, not noticeably narrower than the elytra; pronotum slightly bisinuate basally; hypomeron strongly inflexed into more or less horizontal plane

throughout, only narrowly visible or not visible in lateral aspect; abdominal terga III-V with moderate to deep transverse basal impressions (some III-VI); male sternum VI without lobate projection on posterior margin; male sternum VII with broad band of numerous sensory pores basally,



Figs. 28-34. *Phymatura brevicollis* (Kraatz). 28, Head, dorsal aspect. 29, Labrum, dorsal aspect. 30, Labrum, epipharyngeal region. 31, Mandible, ventral aspect. 32, Maxilla, ventral aspect. 33, Lacinia of maxilla, dorsal aspect. 34, Labium, ventral aspect. (Scale line = 0.1 mm.)

without concentration of setose sensory pores basally (Fig. 37); posterior triangular projection of male sternum VIII with asetose posterior margin (Fig. 38); median lobe of aedeagus with slender, spinose apical process and slender and pointed flagellum, without pair of sclerotized structures on internal sac (Figs. 41, 46).

Description (Fig. 27).—Lengths of adults 2.3–4.0 mm. Body relatively broad in dorsal outline, slightly depressed, slightly narrowed anteriorly and posteriorly. Surface sculpture reticulate to virtually absent, surface shiny or not. Body microsetae fine, moderately dense, more or less uniformly distributed, punctures moderate in size, dense, uniformly distributed, not asperite. Macrosetae inconspicuous.

Head (Fig. 28).—Broad, transverse, noticeably narrower than apex of pronotum to virtually as wide as apex of pronotum. Head not narrowed behind eyes, neck absent. Integumental sculpture slightly reticulate to virtually absent. Punctures moderate sized, round. Setation moderately dense, directed medially and anteriorly. Eyes very large to moderate in size, 2.0–1.2 times length of temple. Infraorbital carina markedly developed, complete. Antenna elongate to short, slightly incrassate toward apex or parallel-sided; article 4 transverse to elongate, similar to articles 1 to 3 in examined representatives, article 5 transverse to elongate; article 10 slightly elongate to transverse; antennal articles 5 to 10 increasing in relative lengths more apically in examined representatives.

Mouthparts.—Labrum (Figs. 29, 30) with epipharyngeal area with medial pores small to very small, numerous, evenly dispersed in longitudinal sensory field. Mandibles with abcondylar molar patch of denticles large, denticles moderate-sized to very small, dense (Fig. 31). Maxilla (Figs. 32, 33) with teeth in apical 0.25 of lacinia arranged in a single row of widely dispersed teeth; apex of galea with 7 to 8 rows of unmodified (setose) setae. Labium (Fig. 34) typical of subtribe; ligula with pair of sensory setae small or absent; two medial setae of prementum present, arranged one directly behind the other; medial setal insertions close to moderately distant; medial pseudopore field narrow, without pseudopores.

Thorax.—Pronotum broad, transverse, 1.4–1.5 times as wide as long, slightly convex in dorsal outline; about as wide at base as base of elytra; postero-lateral angles moderately to sharply angulate; base slightly to moderately bisinuate; punctures small, round, numerous, setation fine, moderate to densely distributed; integument slightly reticulate. Elytra with postero-lateral angles moderately sinuate; punctures moderate in size, dense, lunulate (open behind); microsetae dense, moderately fine. Wings with setose lobe on flabellum various, 3–6 (Fig. 36). Hypomeron strongly inflexed throughout, not, or only narrowly, visible in lateral aspect; hypomeron contacting lateral border of pronotum at or very near antero-lateral angles

of pronotum. Mesosternal medial carina strong, present in anterior 0.2–0.5 of mesosternum. Mesocoxal cavities moderately separated by meso- and metasternal processes (Fig. 35); relative lengths mesosternal : isthmus : metasternal processes about 4.0–4.5 : 0.5 : 3; apex of mesosternal process narrow, obtusely pointed, apex of metasternal process acutely to broadly rounded. Hind tarsomere I moderately long, about as long as II and III together.

Abdomen.—Slightly tapered apically to broadly pointed apex; terga IV–V (VI slightly in some) with moderate transverse basal impressions; punctures moderately large, lunulate, dense; microsetae fine, densely distributed; microsetae on basal terga directed posteriorly; macrosetae inconspicuous. Sterna III–V with slight transverse basal impressions.

Secondary Sexual Characteristics.—Males: elytron without carina near suture or small knob at sutures about 0.4 length of elytron from posterior edge; tergum VII (Figs. 39, 45) with long prominent medial carina to short prominent medial carina; tergum VIII (Figs. 39, 45) broadly emarginate posteriorly, with 4 to 5 denticles in emargination on each side of midline, denticles moderate to large in size; dorsum of tergum VIII with moderately long medial carina, short, but distinct, medial carina, or small medial tubercle; sternum VI without small medial lobe on posterior margin; sternum VII (Fig. 37) with broad band of sensory pores basally (visible in microslide preparations), without concentration of setose glandular pores medially, sternum VIII (Fig. 38) with posterior triangular projection, projection with asetose posterior margin.

Aedeagus.—Paramere (Figs. 40, 47) with apical lobe of paramerite relatively short (<0.5 times length of paramerite) to long (0.8 times length of paramerite), setae 1 to 4 of apical lobe of paramerite long or short, not clustered near tip. Aedeagus (Figs. 41, 46) with apical lobe elongate, slender; internal sac without sclerotized internal plates; flagellum moderately long, tapering to an acute apex.

Spermatheca (Figs. 42, 43, 44).—Basal bulb simple, apex rounded; neck bent (90° to more or less straight; spermathecal tube membranous, more or less straight (Fig. 42) or very long and convoluted (Fig. 44). Vaginal sclerotization slight, less than to about 0.5 complete circle of sclerotized cuticle.

Discussion.—About 15 species have been described in either *Phymatura* or *Venusia*. Among *Phymatura* I have examined five species (*Phymatura brevicollis* Kraatz from Europe and *P. picta* Cameron, *P. intermedia* Cameron, *P. juncunda* Cameron and *P. aspericeps* Cameron from India) that are correctly placed in this genus. Other *Phymatura* that I have not examined, have been described from southeast Asia (*P. orientalis* Cameron, *P. malaisei* Scheerpeltz), Japan (*P. japonica* Cameron), Nepal (*P. suturalis* Pace), and South America (*P. dubiosa* Bernhauer, *P. barbiellini* Bernhauer,

and *P. brasiliana* Bernhauer). Casey (1906) described two new species of *Venusia* from eastern North America (*Venusia picta* and *V. lactula*) and transferred *Bolitochara blanchardi* Casey to *Venusia*. There appears to be only a single valid species, *Venusia picta* Casey (= *Bolitochara blanchardi* Casey).

The species of *Phymatura* and *Venusia* included in the phylogenetic analysis were shown to form a monophyletic group in all but one of the analyses. The derived features in the aedeagus of all examined members of these taxa provide strong evi-

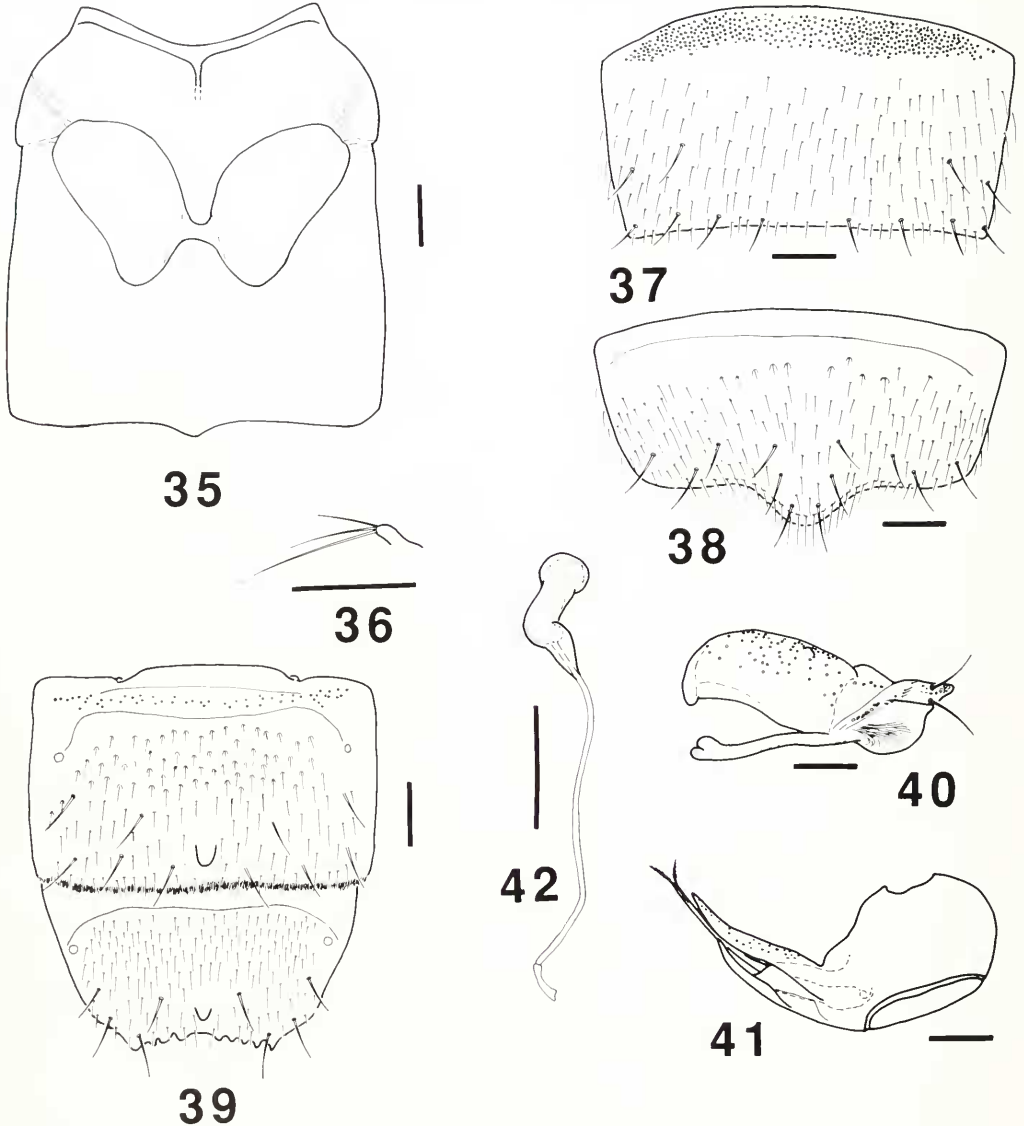
dence of their monophyly (see phylogenetic analysis).

Phymatura is the sister group to *Neotobia* new genus in some of the phylogenetic analyses (figs. 2, 5) but not in others (Figs. 3, 4).

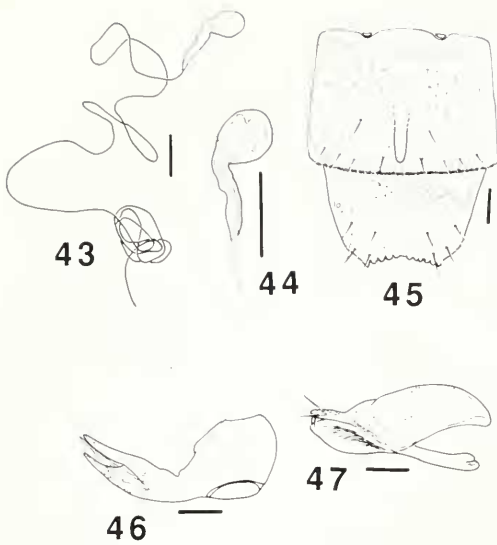
Genus *Pleurotobia* Casey

(Figs. 48-67)

Pleurotobia Casey 1906, p. 273. Type species *Pleurotobia suturalis* Casey. Fixed by Fenyes 1918, p. 24.—Casey



Figs. 35-42. *Phymatura brevicollis* (Kraatz). 35, Meso-metasternum, ventral aspect. 36, Flabellum of wing. 37, Male, sternum VII. 38, Male, sternum VIII. 39, Male, terga VII-VIII. 40, Male, paramere, external aspect. 41, Male, median lobe of aedeagus, lateral aspect. 42, Female, spermatheca. (Scale line = 0.1 mm.)



Figs. 43-47. *Phymatura* (= *Venusa*) *blanchardi* (Casey). **43.** Female, spermatheca, outline showing long, convoluted spermathecal duct. **44.** Female, spermathecal bulb, detail. **45.** Male, terga VII-VIII. **46.** Male, median lobe of aedeagus, lateral aspect. **47.** Male, paramere, external aspect. (Scale line = 0.1 mm.)

1906: 273.—Fenyés 1920: 114 (as a synonym of *Ditropalia* Casey).—Seevers 1978: 164 (as a synonym of *Bolitochara* Mannerheim).
Phymaturosilusa Roubal 1932, p. 178. Type species *Phymaturosilusa magnifica* Roubal 1932, p. 178, by monotypy.—Roubal 1932: 178.—Smetana 1957: 322.—Lohse 1974: 61.

Pleurotobia can be easily recognized by the combination of: head broad with very large eyes, eyes 1.3-1.5 times as long as length of temples; head not at all narrowed behind the eyes to form a neck; moderately long antenna with antennomeres 5 to 10 transverse to elongate, longer in males than in females; pronotum broad, transverse, 1.4-1.5 times as wide as long; hypomeron inflexed into near horizontal plane basally but deflexed to near vertical in apical half, at least apical half broadly visible in lateral aspect; pronotum not noticeably narrower than elytra, slightly bisinuate basally; mesocoxal cavities broadly separated by intercoxal processes (Fig. 56), apex of mesosternal process broadly rounded; terga III-V with moderate transverse basal impressions; sterna III-V with slight transverse basal impressions; male sternum VI (Figs. 58, 59) with medial setose lobate projection on posterior margin; male sternum VII (Figs. 58, 59) with concentration of setose pores medially, as well as band of numerous sensory pores basally; triangular projection of male sternum VIII (Fig. 58) without asetose posterior margin; most with tergum VII (Figs. 60, 64) with 2 to 3 oblique to posteriorly directed carinae on each side of midline

(reduced in some); tergum VIII (Figs. 60, 64) with medial carina and 1 to 2 lateral carinae on each side; median lobe of aedeagus (Figs. 62, 66), with large, tentlike apical process, two platelike structures on internal sac, and tubelike flagellum.

Description (Fig. 48).—Lengths of adults 3.0-5.0 mm. Body relatively broad and elongate in dorsal outline, more or less parallel-sided and convex in cross section. Surface sculpture faintly reticulate, body more or less shiny. Body moderately densely pubescent with fine microsetae. Body moderately densely punctured, punctures coarse to fine, asperite or not. Macrosetae inconspicuous.

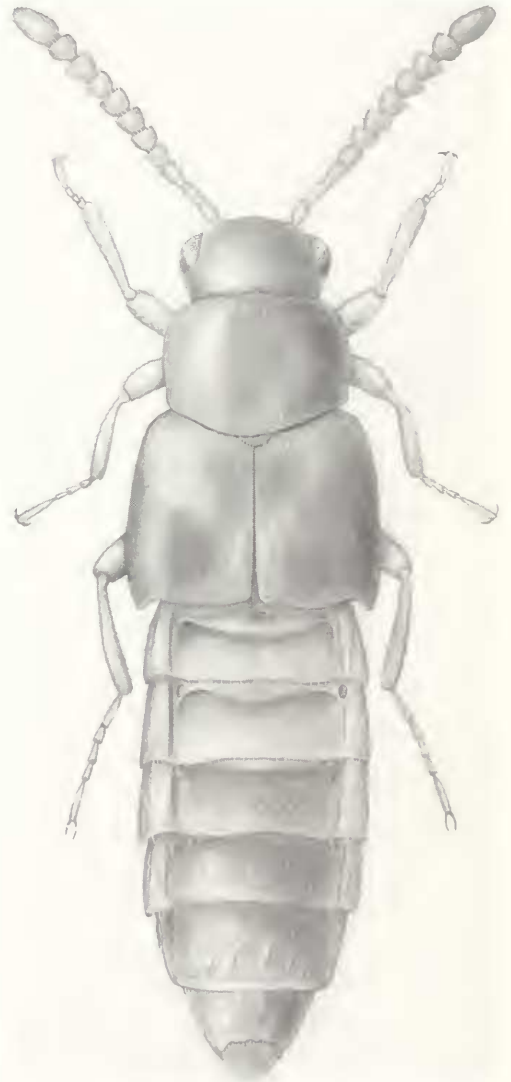
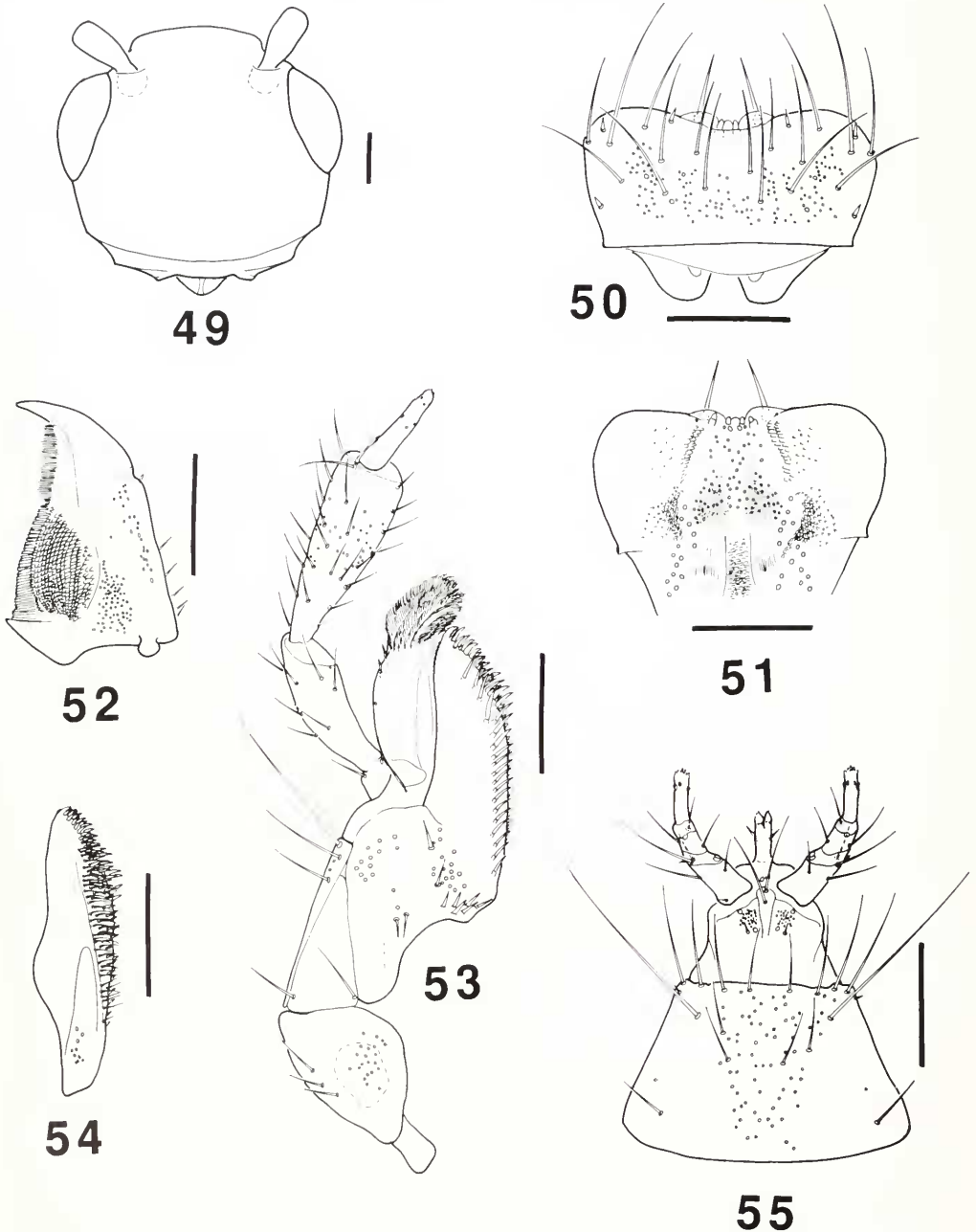


Fig. 48. *Pleurotobia trimaculata* (Erichson). Habitus. Length = 4.5 mm.

Head (Fig. 49).—Broad, almost as wide as apex of pronotum. Head not narrowed behind eyes, neck absent. Integumental sculpture faint to absent, surface shiny. Punctures large to small, densely distributed, round; setae directed medi-

ally and anteriorly or virtually all directed medially. Eyes large to moderately large, eye length 1.5–1.3 times length of temple. Infraorbital carina complete, markedly developed. Antenna moderately elongate, more or less parallel-sided



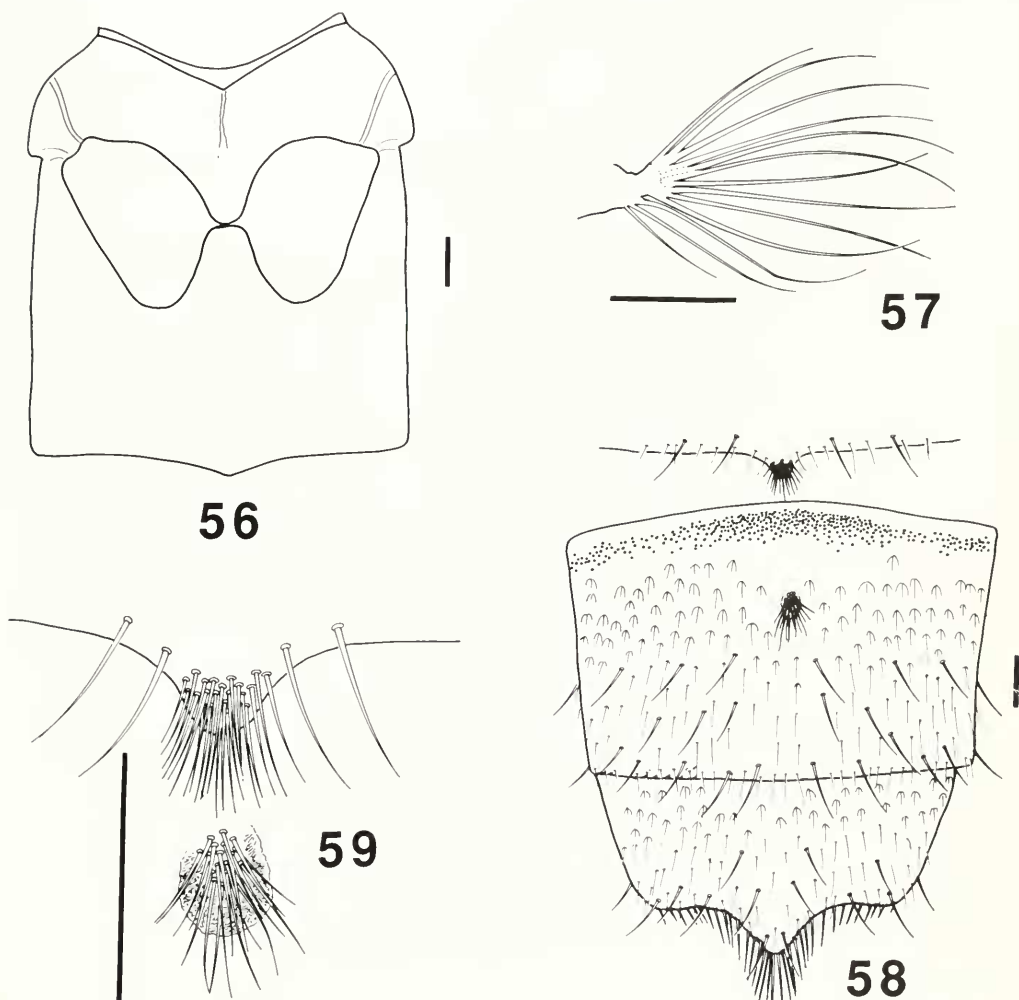
Figs. 49–55. *Pleurotobia trimaculata* (Erichson). 49, Head, dorsal aspect. 50, Labrum, dorsal aspect. 51, Labrum, epipharyngeal region. 52, Mandible, ventral aspect. 53, Maxilla, ventral aspect. 54, Lacinia of maxilla, dorsal aspect. 55, Labium, ventral aspect. (Scale line = 0.1 mm.)

from article 5 to 10, not noticeably incrassate; antennal structure different in males and females (see secondary sexual characteristics below); article 4 elongate to quadrate, similar in setation and sculpture to articles 1 to 3 or 5 to 10; article 5 elongate to transverse; article 10 transverse to quadrate; antennal articles 5 to 10 decreasing in relative lengths more apically.

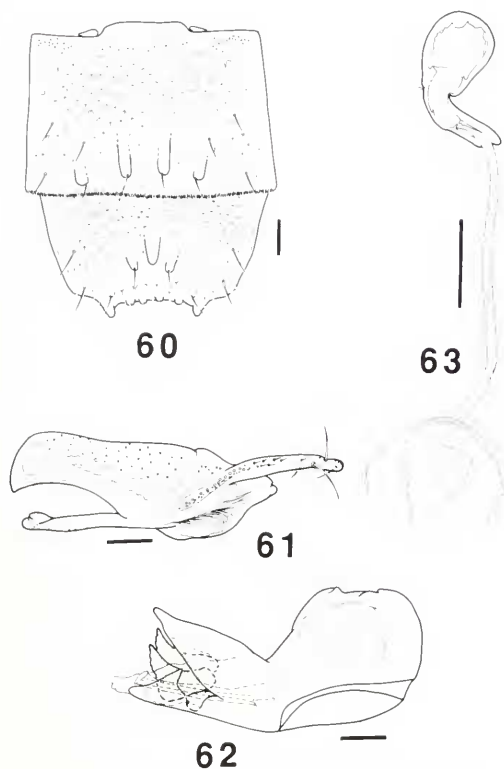
Mouthparts.—Labrum (Figs. 50, 51) with epipharyngeal area similar to that of *Bolitochara*. Mandibles with abcondylar molar patch of denticles large, denticles moderate sized to small, very numerous, densely arranged (Fig. 52). Maxilla (Fig. 53) with teeth on apical 0.25 of lacinia arranged into 3 to 4 irregular rows and densely arranged near apex (Fig. 54); apex of galea with 10 to 12 rows of unmodified (setose) setae (Fig.

53). Labium (Fig. 55) typical of subtribe; ligula with pair of sensory setae large; two medial setae present on prementum, bases arranged one directly behind the other, setal insertions moderately separated; medial pseudopore field of prementum narrow, without pseudopores.

Thorax.—Pronotum broad, transverse, 1.4–1.5 times as wide as long, slightly convex in dorsal outline; almost as wide at base as base of elytra; postero-lateral angles sharply angulate; base slightly to moderately bisinuate; punctures small to large, round, numerous; microsetae fine, moderately dense; microsculpture slightly to moderately reticulate. Elytra with postero-lateral angles moderately to strongly sinuate; punctures large, numerous, lunulate; setae fine, moderately dense. Wings with large flabellum with 11 to 13 setose



Figs. 56–59. *Pleurotobia trimaculata* (Erichson). 56, Meso-metasternum. 57, Flabellum of wing. 58, Male sternal features, posterior margin of sternum VI, sterna VII and VIII. 59, Male, detail of setose lobe of sternum VI and concentration of setose pores on sternum VII. (Scale line = 0.1 mm.)



Figs. 60-63. *Pleurotobia trimaculata* (Erichson). 60, Male, terga VII-VIII. 61, Male, paramere, external aspect. 62, Male, median lobe of aedeagus, lateral aspect. 63, Female, spermatheca and vaginal sclerotization. (Scale line = 0.1 mm.)

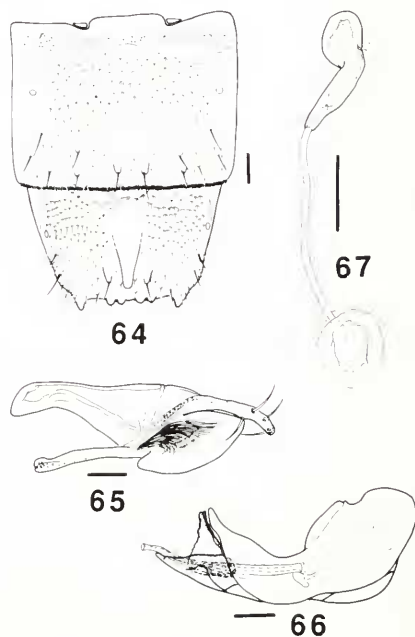
lobes (Fig. 57). Hypomeron broadly visible in lateral aspect, inflexed posteriorly and deflexed almost vertically anteriorly, hypomeron contacting lateral line of pronotum slightly posteriorly to anterolateral angles. Mesosternal medial carina (Fig. 56) markedly developed, spreading to lateral angles of mesosternal process near apex of process or fading in apical 0.25 of process. Mesocoxal cavities widely separated by meso- and metasternal processes (Fig. 56); relative lengths mesosternal : isthmus : metasternal processes 5.5 : 0-5 : 4.5; apex of mesosternal process slightly rounded, apex of metasternal process truncate. Hind tarsomere I long, about as long as II and III together.

Abdomen.—Robust, more or less parallel-sided; terga III-V (VI slightly) with deep basal transverse impressions; punctures numerous, large to moderately large, lunuate; microsetae fine, numerous, more or less densely arranged, macrosetae inconspicuous. Sterna III-V with slight transverse basal impressions.

Secondary Sexual Characteristics.—Males: each elytron with markedly to moderately developed carina near suture, variously developed in different

males, up to 0.5 times length of suture; tergum VII (Figs. 60, 64) with 2 to 3 oblique to posteriorly directed carinae on each side of midline, variously developed in different males, some with most lateral carinae reduced to small asperity or completely absent; tergum VIII (Figs. 60, 64) broadly and distinctly emarginate posteriorly, with 2 to 3 moderate-sized to robust denticles in emargination on each side of midline; dorsum of tergum VIII with medial carina and 1 to 2 smaller lateral carinae on each side; sternum VI (Figs. 58, 59) with small medial lobe on posterior margin, medial lobe setose; sternum VII (Figs. 58, 59) with concentration of setose glandular pores medially, porose area large, as well as broad band of sensory pores basally, with concentration of setose glandular pores medially, porose area large; sternum VIII (Fig. 58) with posterior triangular projection, projection without asetose posterior margin. Antennal articles of males relatively longer than comparable articles of females.

Aedeagus.—Paramere (Figs. 61, 65) with apical lobe of paramerite moderately long, 0.8-0.5 times length of paramerite; setae 1 to 4 of apical lobes moderate length to long, not clustered near tip. Aedeagus (Figs. 62, 66) with apical lobe large, tentlike; internal sac with pair of large sclerotized platelike structures; flagellum of moderate length, tubular.

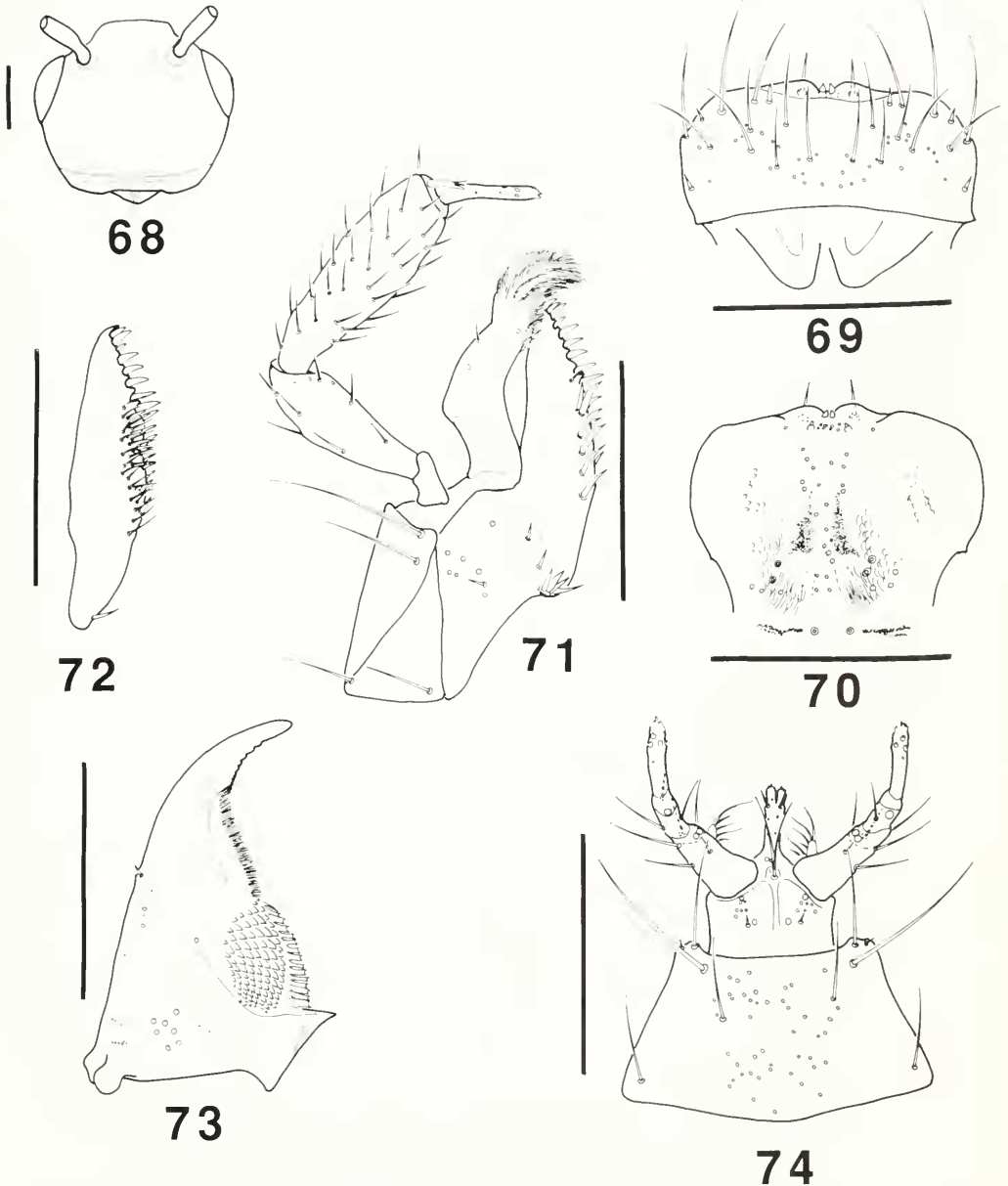


Figs. 64-67. *Pleurotobia* (= *Phymaturosilus*) *magna* Roubal. 64, Male, terga VII-VIII. 65, Male, paramere of aedeagus, external aspect. 66, Male, median lobe of aedeagus, lateral aspect. 67, Female, spermatheca and vaginal sclerotization. (Scale line = 0.1 mm.)

Spermatheca (Figs. 63, 67).—Basal bulb simple, apex rounded; neck only slightly bent to bent about 60° from straight. Spermathecal tube membranous, more or less straight. Vaginal sclerotization markedly developed; about 0.75 to almost complete circle of sclerotized tissue.

Discussion.—Casey (1906) described three species in his new genus *Pleurotobia* from eastern

North America (*P. suturalis* Casey, *P. tristigma* Casey, and *P. texana* Casey). I have examined the types of all three of these species and cannot find any significant difference among them. They all appear to be synonymous with *Bolitochara trimaculata* Erichson. *Pleurotobia tristigmata* (Erichson) reported by Ashe (1990) is an error for *Pleurotobia tristigma* Casey. There is an undescribed species of



Figs. 68–74. *Pseudatheta elegans* Cameron. 68, Head, dorsal aspect. 69, Labrum, dorsal aspect. 70, Labrum, epipharyngeal aspect. 71, Maxilla, ventral aspect. 72, Lacinia of maxilla, dorsal aspect. 73, Mandible, ventral aspect. 74, Labium, ventral aspect. (Scale line = 0.1 mm.)

Pleurotobia (here reported as "*P. sp. A*") from Oklahoma.

The single known species of *Phymatosilusa*, *P. magnifica* Roubal, is only known from central Europe. As noted above (see Phylogeny), there is good evidence that *Pleurotobia* and *Phymatosilusa* are synonyms.

Members of the genus are only known to occur in the eastern half of North America and central Europe.

Genus *Pseudatheta* Cameron

(Figs. 68-79)

Pseudatheta Cameron 1920, p. 224. Type species *Pseudatheta elegans* Cameron 1920, p. 224, by monotypy.—Cameron 1920: 224.—Cameron 1932: 141.—Cameron 1939a: 224.

Diagnosis.—Members of *Pseudatheta* can be recognized by: small size, length 1.5-2.0 mm, eyes large, as long as length of temples; head not narrowed behind eyes to form a neck (Fig. 68); antenna slightly incrassate, pronotum very broad, 1.5 times as wide as long, not noticeably narrower than elytra; hypomeron inflexed into horizontal plane throughout, not visible in lateral aspect; mesosternum without medial longitudinal carina; mesocoxal cavities narrowly separated by intercoxal processes, mesosternal process slender and acutely pointed (Fig. 75); hind tarsomere I not significantly longer than II; only abdominal tergal III-IV moderately impressed at base; sterna not basally impressed; male sternum VI without medial lobate projection on posterior margin; male sternum VII (Fig. 76) with broad band of sensory pores basally, without medial concentration of setose sensory pores; triangular projection of posterior margin of male sternum VIII (fig. 76) without asetose posterior margin; median lobe of aedeagus (Fig. 79) with slender, pointed apical process, flagellum tapered to an acute apex, without sclerotized plates on internal sac.

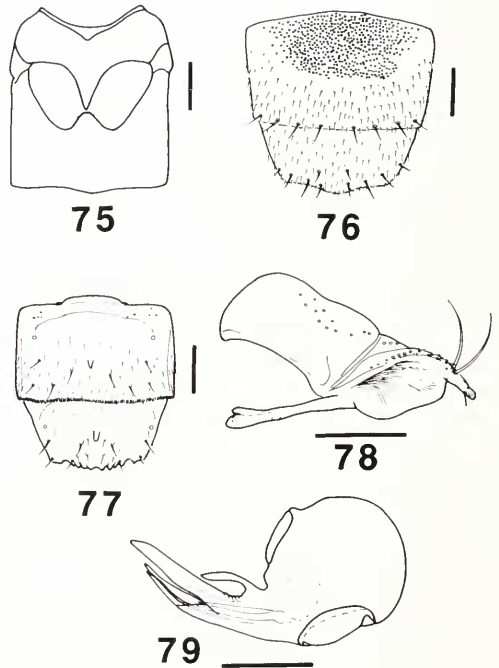
Description.—Lengths of adults 1.5-2.0 mm. Body relatively broad and somewhat flattened, more or less parallel-sided and slightly narrowed behind, to slightly robust. Surface sculpture absent to slight, surface shiny or not. Body finely and moderately pubescent. Punctures of moderate size, densely distributed. Macrosetae inconspicuous.

Head (Fig. 68).—More or less oval, slightly less broad than apex of prothorax; not narrowed behind, without neck. Sculpture absent to slight, surface shiny or not. Punctures large, round. Microsetae directed medially. Eyes moderately large, length about equal to length of temple. Infraorbital carina markedly developed, complete. Antenna moderately short, incrassate toward apex; article 4 transverse, similar in setation and sculpture to 1 to 5; article 5 transverse; article 10 transverse; articles 5 to 10 about equal in relative length.

Mouthparts.—Labrum (Figs. 69, 70) with epi-

pharyngeal area with medial pores small, distant in medial longitudinal sensory field. Mandibles with abcondylar molar patch of denticles large, denticles small, densely arranged (Fig. 73). Maxilla (Figs. 71, 72) with teeth in apical 0.25 arranged in single row of distantly spaced teeth; apex of galea typical of subtribe, setae unmodified. Labium (Fig. 74) typical of subtribe; ligula with pair of sensory setae very small; prementum with two medial setae, medial setae arranged one directly behind the other, setal insertions close, medial pseudopore field narrow, without pseudopores.

Thorax.—Pronotum broad, transverse, about 1.5 times as wide as long, rather flat in dorsal outline; about as wide at base as base of elytra; postero-lateral angles rounded; base broadly rounded, not bisinuate; punctures moderate sized, round, numerous, dense; integument without microsculpture or slightly reticulate. Elytra with postero-lateral angles moderately sinuate; punctures large, densely arranged, lunulate; microsetae fine, moderately dense. Wings without flabellum, without setose lobes. Hypomeron strongly inflexed throughout, not visible in lateral view. Mesosternum without medial carina. Mesocoxal cavities narrowly separated by meso- and metasternal processes (Fig. 75); relative



Figs. 75-79. *Pseudatheta elegans* Cameron. 75, Meso-metasternum. 76, Male, sterna VII-VIII. 77, Male, terga VII-VIII. 78, Male, paramere of aedeagus, external aspect. 79, Male, median lobe of aedeagus, lateral aspect. (Scale line = 0.1 mm.)

lengths mesosternal : isthmus : metasternal processes about 5 : 0 : 2; apex of mesosternal process pointed, apex of metasternal process rounded. Hind tarsomere I short, only slightly longer than II.

Abdomen.—Slightly narrowed apically to broadly pointed apex; terga III–IV with transverse basal impressions. Punctures moderate in size, round, not lunulate; microsetae numerous, more or less dense. Sterna without noticeable transverse basal impressions.

Sexual Characteristics.—Males: each elytron with small to minute tubercle near suture; tergum VII (Fig. 77) with transverse rows of small tubercles or with short medial carina; tergum VIII (Fig. 77) truncate, not incised, with four denticles on each side of midline on apical margin, lateral denticle separated from others by slight gap; dorsal surface of tergum VIII with small medial

tubercle and scattered lateral asperities; sternum VI without small medial lobe in posterior margin, sternum VI and VII (Fig. 76) with very broad band of numerous sensory pores which takes up most of ventral surface of tergum; sternum VIII (Fig. 76) with very slight posterior triangular projection, projection without asetose posterior margin.

Aedeagus.—Paramere (Fig. 78) with apical lobe of paramerite short, length less than 0.5 times length of paramerite; setae 1 to 4 of apical lobe moderate in length, not clustered near the tip. Aedeagus (Fig. 79) with slender pointed apical process; internal sac without sclerotized internal plates; flagellum moderately long, tapered to an acute apex.

Spermatheca.—Not examined.

Discussion.—The genus *Pseudatheta* is known from six species from southeast Asia (*P. elegans* Cameron), *P. indica* Cameron), Africa (*P. africana* Cameron) and Nepal (*P. smetanai* Pace, *P. mendica* Pace and *P. ghoropanesis* Pace). Pace (1989) recently described the three species from Nepal. His illustrations indicate that the aedeagi of these species are somewhat similar to that of *P. elegans*. This suggests that they may be correctly placed in *Pseudatheta*. However, they differ somewhat in external appearance from the generic description provided here. Most notably, *P. ghoropanesis* is larger (3.7 mm in length), and has smaller eyes, longer temples and a head which is slightly narrowed behind. If, after examination, these species prove to be correctly placed in *Pseudatheta*, then the generic description provided here will require modification.

Only the type species of *Pseudatheta* (*P. elegans*) is included in the phylogenetic analysis. Its phylogenetic position is uncertain. Various analyses either place it as the sister group to *Austrasilida* new genus (Fig. 2), sister group to *Pleurotobia* + *Bolitochara* (Fig. 4) or the most basal lineage in the subtribe (Fig. 5).

Genus *Silusida* Casey

(Figs. 80–94)

Silusida Casey 1906, p. 270. Type species *Silusida marginella* Casey. Fixed by Fenyés 1918, p. 25.—Casey 1906: 270.—Fenyés 1920: 116.—Notman 1920: 713.—SeEVERS 1978: 164 (as a synonym of *Bolitochara* Mannerheim).

Diagnosis.—Members of *Silusida* can be recognized by the combination of: head (Fig. 81) broad, with moderately large eyes, eye size 1.3–1.5 times as long as temple; head not at all narrowed behind the eyes to form a neck; pronotum broadly transverse, 1.5 times as wide as long; short incrassate antenna with antennomeres 5 to 10 transverse; basal angles of pronotum broadly rounded, not angulate; pronotum not noticeably narrower than elytra; hypomeron inflexed into horizontal plane throughout, only narrowly visible in lateral aspect; abdominal terga III–VI with moderate transverse basal im-

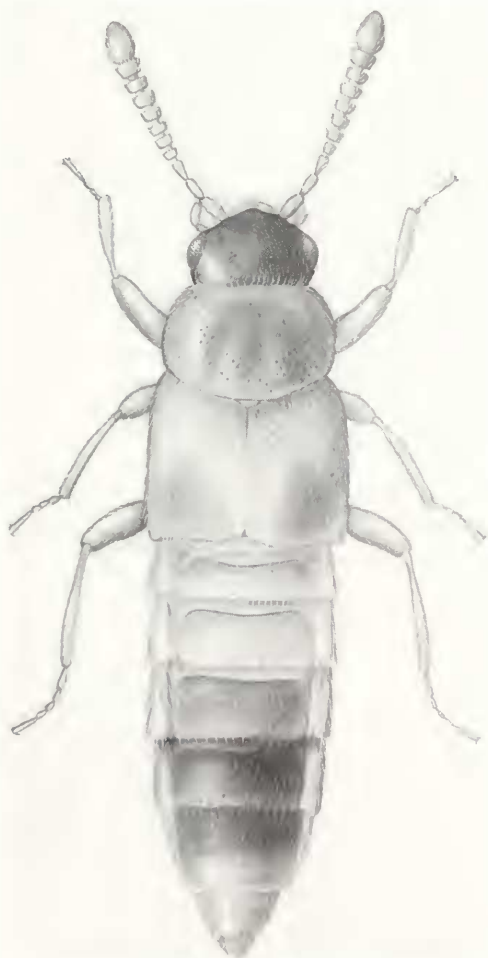
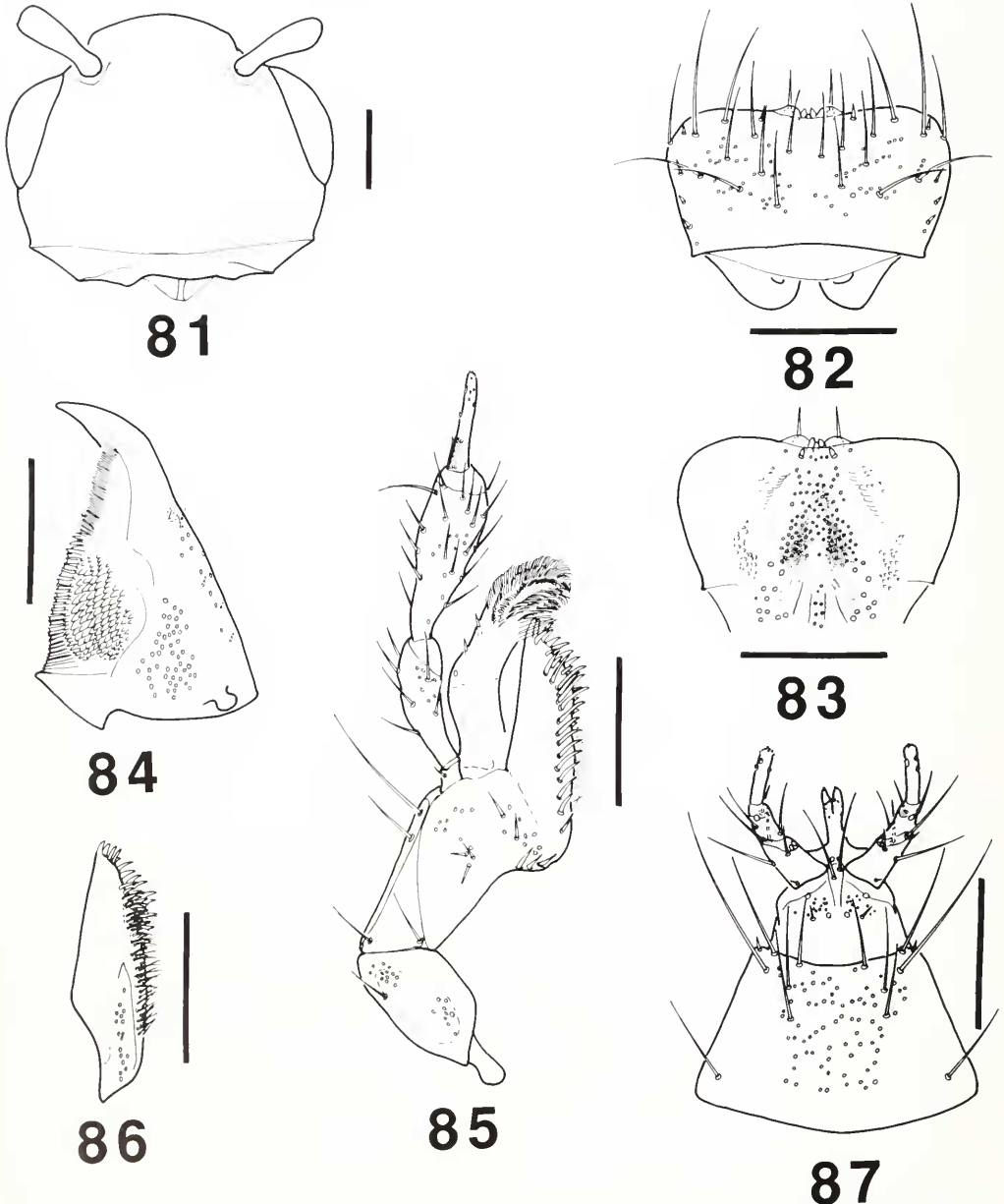


Fig. 80. *Silusida marginella* Casey. Habitus. Length = 2.5 mm.

pressions; sterna not noticeably impressed basally; male sternum VI without medial lobate projection on posterior margin; male sternum VII (Fig. 90) with broad band of numerous sensory pores basally, without concentration of setose pores medially; triangular projection of male sternum VIII (Fig. 90) with asetose posterior border; median lobe of aedeagus (Fig. 93)

with apical process large, tentlike, without obvious sclerotized plates on internal sac, and short, tubular flagellum.

Description (Fig. 80).—Lengths of adults 2.1 to 3.0 mm. Body relatively broad, more or less parallel-sided, somewhat depressed in cross section. Surface sculpture faintly reticulate, body not strongly shiny. Body moderately densely pubes-



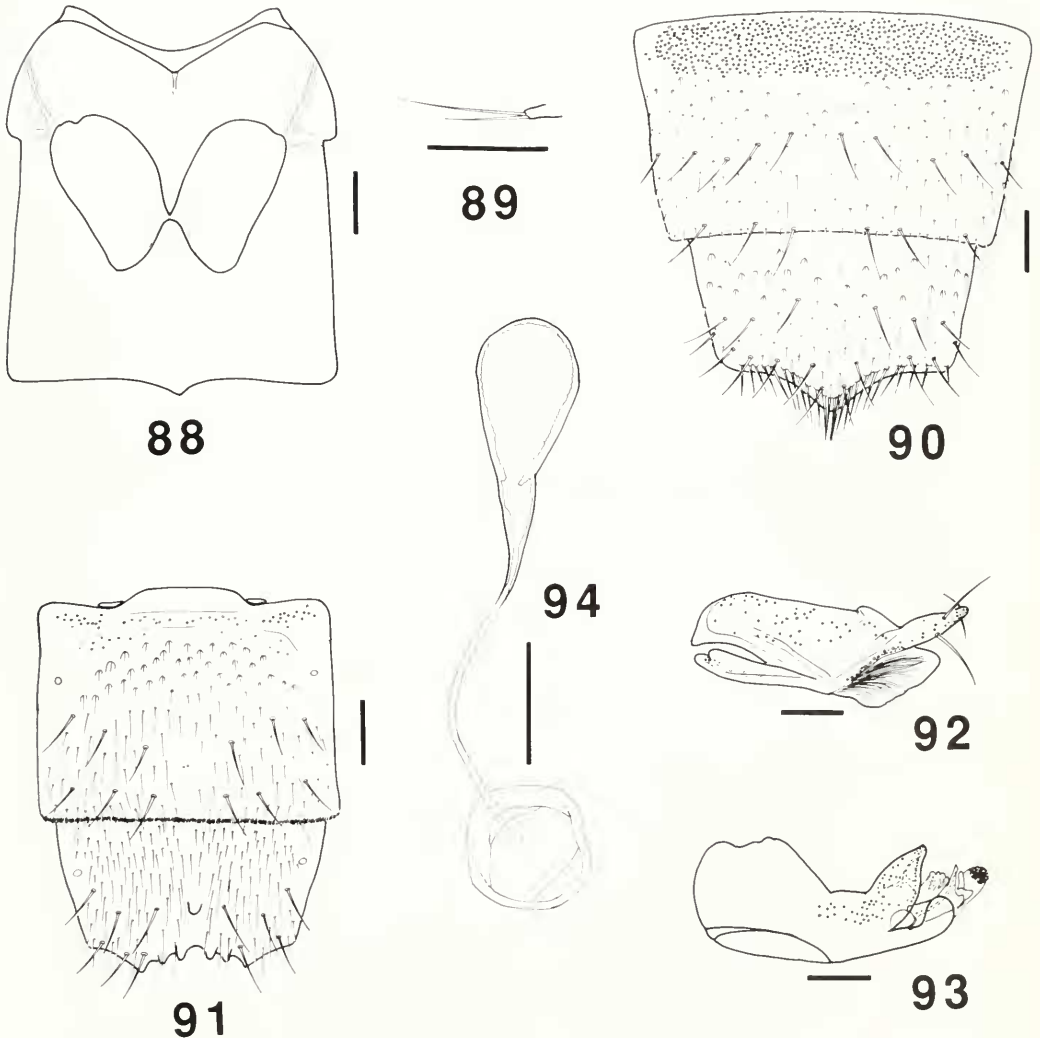
Figs. 81-87. *Silusida marginella* Casey. 81, Head, dorsal aspect. 82, Labrum, dorsal aspect. 83, Labrum, epipharyngeal aspect. 84, Mandible, ventral aspect. 85, Maxilla, ventral aspect. 86, Lacinia of maxilla, dorsal aspect. 87, Labium, ventral aspect. (Scale line = 0.1 mm.)

cent, punctures small, densely and uniformly distributed. Macrosetae inconspicuous.

Head (Fig. 81).—Broad, about as wide as apex of pronotum. Head not narrowed behind the eyes, neck absent. Integumental sculpture slightly reticulate. Punctures small, round, densely distributed; microsetae directed medially and anteriorly. Eyes moderately large, length 1.3–1.5 times length of temples. Infraorbital carina complete, markedly developed. Antenna short, incrassate toward apex from article 4 to 11; article 4 quadrate to slightly transverse, intermediate in sculpture and shape between articles 1 to 3 and 5 to 10; article 5 transverse; article 10 strongly transverse;

antennal articles 5 to 10 decreasing in relative lengths apically.

Mouthparts.—Labrum (Figs. 82, 83) with epipharyngeal area with larger, more distinct pores in longitudinal medial sensory field. Mandibles (Fig. 84) with abcondylar molar patch of denticles large, denticles small, very numerous, densely arranged. Maxilla (Figs. 85, 86) with teeth on apical 0.25 of lacinia arranged in 1 to 2 irregular rows (Fig. 86); apex of galea with 8 to 9 rows of unmodified (setose) setae (Fig. 85). Labium typical of subtribe (Fig. 87); ligula with pair of sensory setae very minute; prementum with two pair of sensory setae, arranged one directly be-



Figs. 88–94. *Silusida marginella* Casey. 88, Meso-metasternum. 89, Flabellum of wing. 90, Male, sterna VII–VIII. 91, Male, terga VII–VIII. 92, Male, paramere of aedeagus, external aspect. 93, Male, median lobe of aedeagus, lateral aspect. 94, Female, spermatheca and vaginal sclerotization. (Scale line = 0.1 mm.)

hind the other, insertions moderately distant; medial pseudopore field narrow, without pseudopores.

Thorax.—Pronotum broad, transverse, about 1.5 times as wide as long, relatively flattened in dorsal outline; almost as wide as base of elytra; postero-lateral angles more or less rounded; base very slightly bisinuate or not noticeably bisinuate; punctures small, numerous, round, setation fine; moderately dense, uniformly distributed; integumental microsculpture slightly reticulate, surface not noticeably shiny. Elytra with postero-lateral angles moderately sinuate; punctures small, numerous, lunulate; microsetae fine, densely and uniformly distributed. Wings with very small flabellum (Fig. 89) with two (a few specimens with three) setose lobes on each. Hypomeron strongly inflexed throughout, only narrowly visible in lateral aspect; anterior margin of hypomeron contacting pronotal lateral line very near antero-lateral angle of pronotum. Mesosternal medial carina (Fig. 88) slightly present in anterior 0.25 to virtually absent in some specimens. Mesocoxal cavities narrowly separated by meso- and metasternal processes (Fig. 88); relative length mesosternal : isthmus : metasternal processes 7 : 1 : 3; apex of mesosternal process acutely pointed, apex of metasternal process broadly rounded. Hind tarsomere I almost as long as II and III together.

Abdomen.—Somewhat broad and flattened, slightly tapered to obtusely pointed apex, terga III-V moderately transversely impressed basally; punctures small, numerous, lunulate; microsetae fine, numerous, moderately densely arranged. Sterna III-V without noticeable transverse basal impressions.

Secondary Sexual Characteristics.—Males: elytra without sutural carina or tubercle; tergum VII (Fig. 91) with faint to small median tubercle or knob; tergum VIII (Fig. 91) broadly and distinctly emarginate posteriorly, with 4 to 5 moderate-sized to small denticles on each side of midline in emargination; dorsum of tergum VIII (Fig. 91) with small to very faint medial knob or tubercle in most, a few specimens without knob or tubercle; sternum VI without small medial lobe on posterior margin; sternum VII (Fig. 90) with broad basal band of numerous sensory pores, without medial concentration of setose sensory pores; sternum VIII (Fig. 90) with moderately developed posterior triangular projection, with asetose posterior margin.

Aedeagus.—Paramere (Fig. 92) with apical lobe of paramerite short, length less than 0.5 times length of paramerite; setae 1 to 4 of apical lobe long, not clustered near apex of lobe. Aedeagus (Fig. 93) with apical process large, tentlike; internal sac without obvious sclerotized plates; flagellum short, tubular.

Spermatheca (Fig. 94).—Basal bulb simple, apex rounded, neck very slightly bent; spermathecal tube membranous, more or less straight; vaginal

sclerotization large, with complete circle of sclerotized cuticle.

Discussion.—Casey (1906) described two species of *Silusida* from eastern North America (*S. marginella* Casey and *S. nanella* Casey). I was not able to locate any specimens of the type series of *S. nanella* in the Casey collection. In addition, *Silusida tenuicornis* Notman from Florida is not a bolitocharine. Therefore, only a single species of *Silusida* can be confirmed for eastern North America.

Silusida is shown to be the sister taxon to *Stictalia* in all phylogenetic analyses. Members of the two taxa differ substantially from each other in numerous derived features of external morphology, secondary sexual characteristics, spermatheca, and aedeagus. Members of the two genera are easily distinguished on the basis of external structure alone. There is no justification for combining them into a single genus.

Genus *Stictalia* Casey

(Figs. 95-114)

Stictalia Casey 1906, p. 234. Type species *Stictalia notata* (Mäklin). Fixed by Fenyés 1918, p. 25.—Casey 1906: 234.—Fenyés 1920: 114 (as a synonym of *Ditropalia* Casey).—Seevers 1978: 164 (as a synonym of *Bolitochara* Mannerheim).

Diagnosis.—Members of *Stictalia* can be recognized by the combination of: eyes moderate sized to small, 1.2-0.5 times length of temples; head slightly narrowed behind eyes to form an inconspicuous neck (Fig. 96) or not obviously narrowed; pronotum only slightly transverse, 1.2-1.3 times as wide as long; pronotum not bisinuate basally; pronotum noticeably to very distinctly narrower than base of elytra; hypomeron moderately to broadly visible in lateral aspect; mesocoxal cavities narrowly to very narrowly separated by intercoxal processes, mesosternal process narrow, acutely pointed apically (Fig. 103); terga III-V or III-VI with moderate to deep transverse basal impressions; sterna III-V with moderate basal impressions or impressions indistinct; many with male secondary sexual characteristics of tergum VII and VIII (Figs. 105, 111) greatly reduced; male sternum VI without VI without medial lobate projection on posterior margin; male sternum VII (Fig. 106) with band of numerous sensory pores basally, without concentration of setose pores medially; triangular projection of male sternum VIII (Fig. 106) with asetose posterior margin; median lobe of aedeagus (Figs. 107, 112, 114) with apical process slender, recurved or foot-shaped, internal sac without obvious sclerotized platelike structures, flagellum tubular; spermatheca distinctive, spermathecal tube sclerotized and distinctively looped (Fig. 109). Known distribution of members of this genus is limited to the west coast of North America, and it is the only genus of the Bolitocharina currently known to occur in that region.

Description (Figs. 95, 110).—Lengths of adults

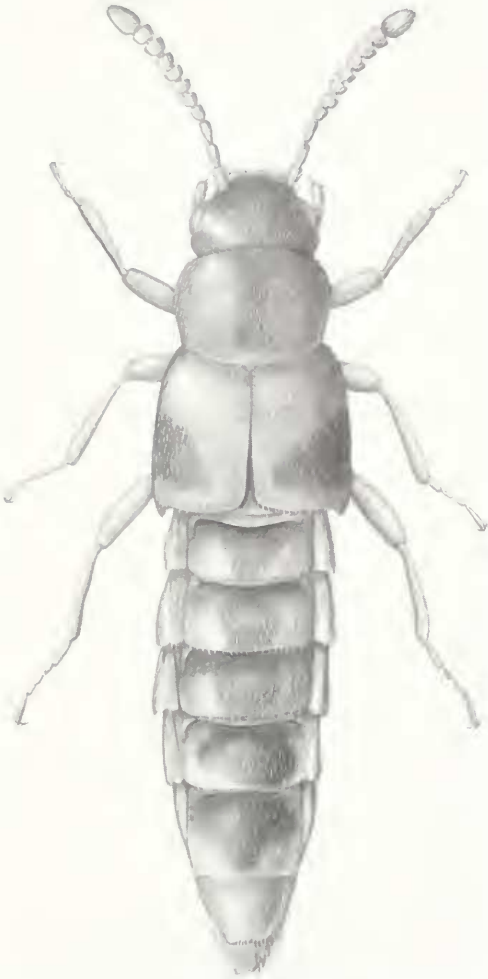


Fig. 95. *Suctalia californica* Casey. Habitus. Length = 3.8 mm.

2.0-4.0 mm. Body form more or less elongate, slender, parallel-sided, somewhat convex in cross section. Surface sculpture various, from moderately reticulate to sculpture absent, surface shiny or not. Body moderately to densely pubescent with fine microsetae; punctation various on different body regions and among species, punctures large and dense to small and more distantly distributed, punctures asperite or not. Macrosetae inconspicuous.

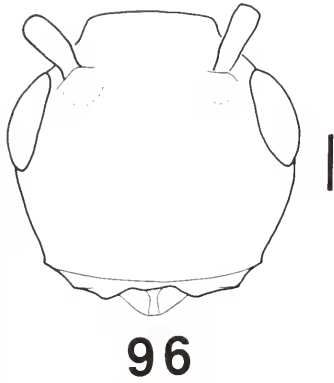
Head (Fig. 96).—More or less oval, quadrate or slightly longer than wide, at most slightly narrowed behind the eyes to produce very broad and inconspicuous neck. Sculpture absent to moderately reticulate, surface shiny or not. Punctures small to moderate sized, numerous, densely distributed, round; microsetae directed medially

and anteriorly or all directed anteriorly. Eyes moderate sized to small, length 1.1-1.2 times length of temples to about 0.5 times length of temples. Infraorbital carina complete, markedly developed. Antenna various, not noticeably incrassate toward apex; article 4 quadrate to elongate, similar in setation and sculpture to articles 1 to 3; article 5 slightly transverse to slightly elongate; article 10 transverse; antennal articles 5 to 10 decreasing in relative lengths toward apex.

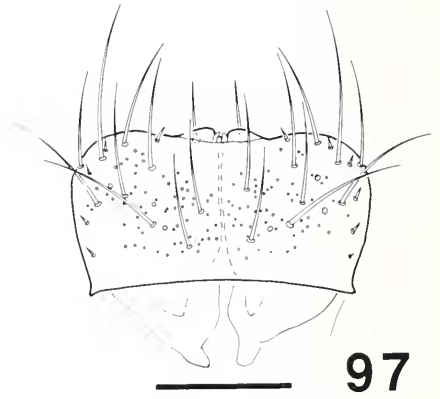
Mouthparts.—Labrum (Figs. 97, 98) with epipharyngeal area with medial pores very small, few, not close, in well-delimited longitudinal sensory field. Mandibles (Fig. 101) with abcondylar molar patch of denticles large, denticles numerous and closely arranged. Maxilla (Figs. 99, 100) with teeth on apical 0.25 of lacinia in 3 to 5 irregular rows, teeth arranged in dense concentration especially near apex (Fig. 100); galeal setae in 6 to 7 rows of unmodified (setose) setae. Labium (Fig. 102) typical of subtribe, ligula without pair of sensory setae; two medial setae present on prementum, bases arranged one directly behind the other, setal insertions moderately distant from each other; medial pseudopore field of prementum narrow, without pseudopores.

Thorax.—Pronotum only slightly transverse, 1.2-1.3 times as wide as long, slightly to markedly convex in dorsal outline; base slightly to distinctly narrower than base of elytra; postero-lateral angles slightly to markedly angulate; base broadly rounded, not bisinuate; punctures large to small, numerous, densely arranged; microsetae fine to relatively stiff, more or less dense; microsculpture various, reticulate to microsculpture absent. Elytra with postero-lateral angles moderately sinuate; punctures moderate to very large, numerous, densely arranged, lunulate; microsetae fine, dense. Wings with very small flabellum (Fig. 104) with 1 (specimens of most species) to 3 (specimens of a few species) setose projections. Hypomeron somewhat inflexed posteriorly to broadly deflexed throughout, moderately to broadly visible in lateral aspect; anterior margin of hypomerion contacting lateral border of pronotum slightly to distinctly posterior to anterior angles of pronotum. Mesosternal medial carina (Fig. 103) various, strong anteriorly and fading in posterior 0.3-0.4 or complete to apex of process. Mesocoxal cavities narrowly to very narrowly separated by meso- and metasternal processes (Fig. 103); relative lengths mesosternal : isthmus : metasternal processes various, from 2.5 : 1 : 1.5 to 6.5 : 1 : 3.5; apex of mesosternal process narrow, acutely pointed; apex of metasternal process acutely rounded. Hind tarsomere 1 long, as long as II and III together.

Abdomen.—Slender, more or less parallel-sided; terga III-V or III-VI with moderate to deep transverse basal impressions, punctures small to large, numerous, densely arranged, lunulate; setae fine, densely arranged to sparse, most taxa with all setae directed posteriorly, some with setae



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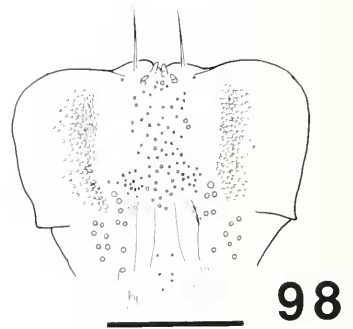
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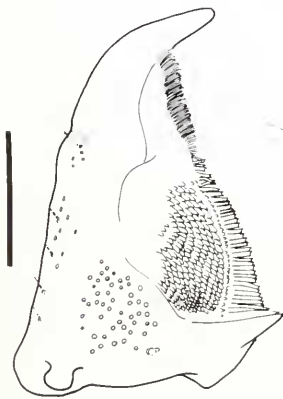
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Figs. 96-102. *Stictalia californica* Casey. 96, Head, dorsal aspect. 97, Labrum, dorsal aspect. 98, Labrum, epipharyngeal aspect. 99, Maxilla, ventral aspect. 100, Lacinia of maxilla, dorsal aspect. 101, Mandible, ventral aspect. 102, Labium, ventral aspect. (Scale line = 0.1 mm.)

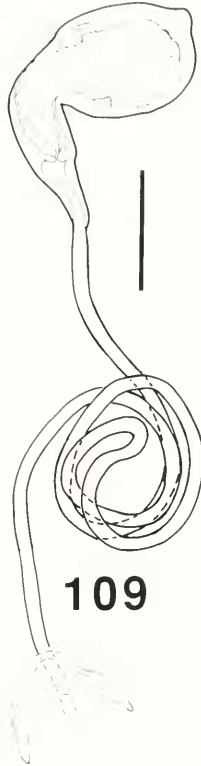
on basal abdominal terga directed obliquely toward midline; integumental microsculpture various, reticulate, obsolete, slightly wavy, or absent. Many with sterna III-V with moderate basal impressions or such impressions indistinct.

Secondary Sexual Characteristics.—Males: elytra without sutural carina or tubercle; tergum VII (Figs. 105, 111) of most with small to moderate

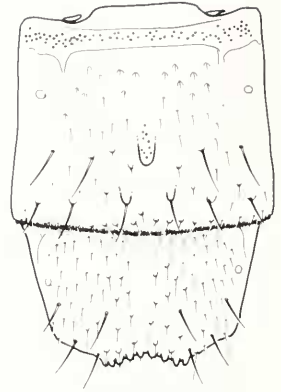
medial knob or tubercle with scattered lateral moderate to minute asperities, some without medial knob and/or asperities; tergum VIII (Figs. 105, 111) with very shallow emargination posteriorly, some with emargination indistinct to absent, with 3 to 4 small to minute denticles on each side of midline in emargination, some with denticles virtually to completely absent, dorsum



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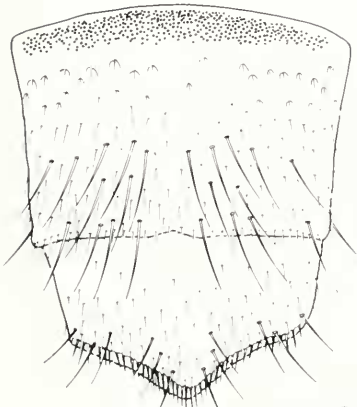
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Figs. 103-109. *Stictalia californica* Casey. 103, Meso-metasternum. 104, Flabellum of wing. 105, Male, terga VII-VIII. 106, Male, sterna VII-VIII. 107, Male, median lobe of aedeagus, lateral aspect. 108, Male, paramere of aedeagus, external aspect. 109, Female, spermatheca and vaginal sclerotization. (Scale line = 0.1 mm.)

of tergum VIII without modification or with very small medial knob or carina and/or scattered asperities; sternum VI without small medial lobe on posterior margin; sternum VII (Fig. 106) with broad basal band of numerous sensory pores, without medial concentration of setose sensory pores; sternum VIII (Fig. 106) with moderately developed posterior triangular projection, with asetose posterior margin.

Aedeagus.—Paramere (Figs. 108, 113) with apical lobe of paramerite very long, length 0.8–1.0 times as long as paramerite; setae 1 to 4 of apical lobe long, not clustered near apex. Aedeagus

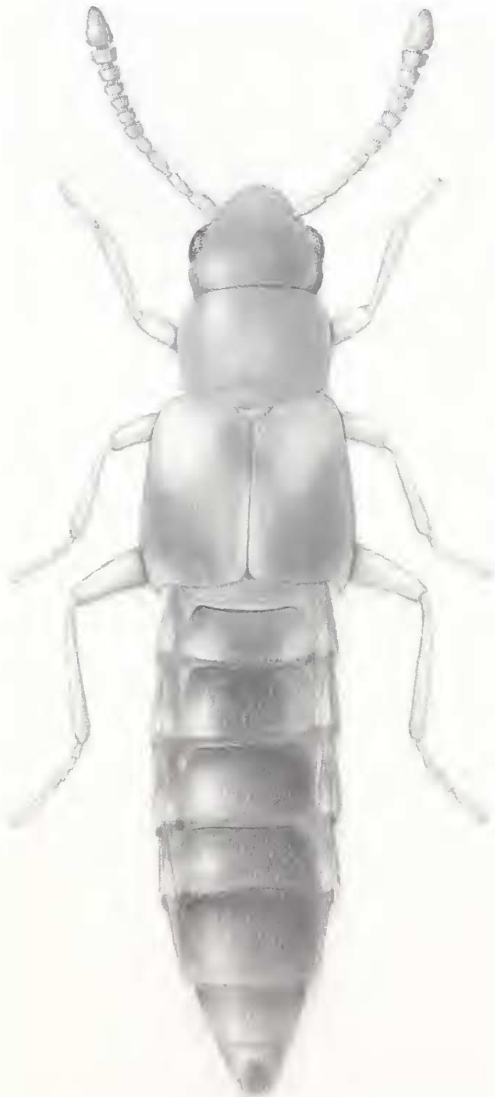


Fig. 110. *Stictalia brevicornis* Casey. Habitus. Length = 3.1 mm.

(Figs. 107, 112, 114) with apical process slender, recurved or footlike; internal sac without distinct pair of platelike sclerotizations but with faint sclerotized areas; flagellum tubular, short or long.

Spermatheca (Fig. 109).—Basal bulb simple, apex with small knob; most with neck bent into angle greater than 90° , a few with neck bent into $30\text{--}60^\circ$ angle; spermathecal tube lightly to moderately sclerotized, arranged in a distinctive pattern of 2 to 3 loops; vaginal sclerotization very small, present as inconspicuous arc of sclerotized cuticle or not visible.

Discussion.—Casey (1906) proposed the genus name *Stictalia* to include 12 new species of bolitocharines from the west coast of North America and included *Bolitochara notata* Mäklin within the group. I have examined all described taxa as well as several undescribed species of *Stictalia*, including specimens of *S. notata* from Alaska and the Queen Charlotte Islands. The species of *Stictalia* included in the analysis form a monophyletic group in all phylogenetic analyses. The type species of *Stictalia*, *S. notata* (Mäklin), was not included in the phylogenetic analysis because of lack of specimens for dissection. However, it is clearly a member of this genus and is very closely related to *S. californica* Casey.

There are two distinct groups of species within *Stictalia*, one exemplified by *S. brevicornis* (provisionally called Type I) (Figs. 110, 111, 112) and one exemplified by *S. notata* (Fig. 114) and *S. californica* (Figs. 95, 105, 107) (provisionally called Type II). These differ in body shape, color pattern, setation, secondary sexual features, and aedeagal features.

Members of *Stictalia* are found on the west coast of North America from Alaska to southern California with one species occurring as far east as Banff, Alberta, in the Canadian Rockies.

Hongophila Ashe, new genus (Figs. 115–131)

Type species *Hongophila arizonica* Ashe.

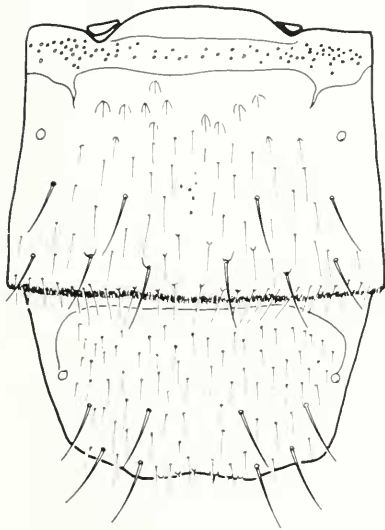
Diagnosis.—Members of *Hongophila* may be recognized by the combination of: eyes moderately large, 1.1–1.2 times as long as length of tempora; head not at all narrowed behind eyes, neck absent; antennomeres 5 to 10 quadrate to transverse; pronotum moderately transverse, 1.4 times as wide as long, not noticeably narrower at base than base of elytra; hypomeron inflexed to near horizontal plane basally and deflexed more vertically anteriorly, anterior half moderately visible in lateral aspect; mesocoxal cavities narrowly separated by intercoxal processes, mesosternal process narrow, pointed apically (Fig. 123); terga III–V with moderate transverse basal impressions; sterna III–V with very slight transverse basal impressions; male sternum VI (Figs. 125, 126) with medial lobate projection on posterior margin, lobate projection asetose; male sternum VII (Figs. 125, 126) without band of numerous

sensory pores basally, with small concentration of setose pores medially; triangular projection of male sternum VIII (Fig. 125) without asetose posterior margin; median lobe of aedeagus (Fig. 128) with apical process elongate, slender, internal sac with pair of spinose and recurved sclerotized plates, flagellum long and tapered to an acute apex. Members of this genus are very difficult to distinguish from those of *Neotobia*. Examination of secondary sexual and aedeagal features are necessary for confident identification of these taxa.

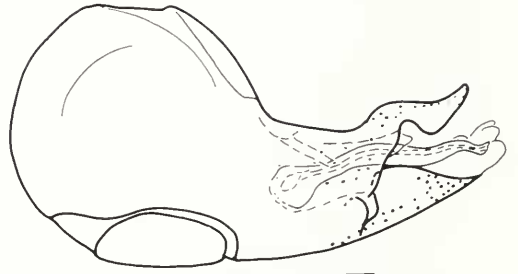
Description. (Fig. 115).—Length of adults 2.8–

3.5 mm. Body more or less narrow and elongate. Surface sculpture distinct, reticulate throughout in known species, body not shiny; punctures very small, numerous, densely and uniformly distributed, microsetae fine, uniformly and densely distributed. Macrosetae inconspicuous.

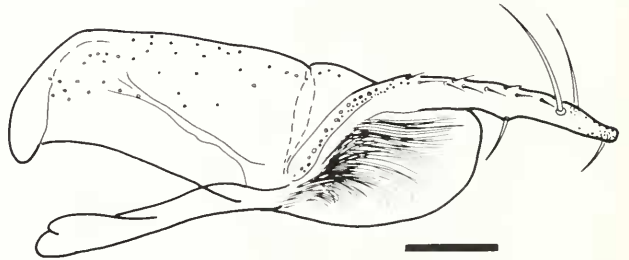
Head (Fig. 116).—Broad, almost as broad as apex of pronotum, not noticeably narrowed behind, neck absent. Surface distinctly reticulate in known species; punctures very small, round, densely distributed. Microsetae directed medially and anteriorly. Eyes moderately large, length 1.1–1.2 times length of temples. Infraorbital ca-



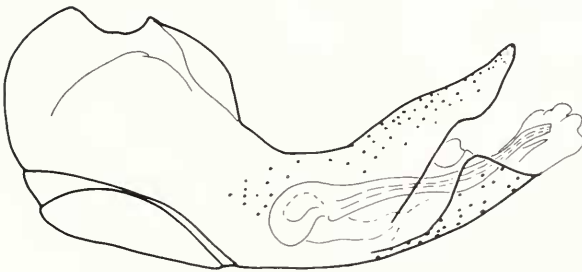
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Figs. 111–113. *Stictalia brevicornis* Casey. 111, Male, terga VII–VIII. 112, Male, median lobe of aedeagus, lateral aspect. 113, Male, paramere of aedeagus, external aspect. (Scale line = 0.1 mm.)

Fig. 114. *Stictalia notata* (Mäklin), male, median lobe of aedeagus, lateral aspect. (Scale line 0.1 mm.)

rina markedly developed, complete. Antenna moderately elongate, slightly incrassate toward apex; article 4 slightly elongate, similar to articles 1 to 3 in setation and sculpture; article 5 more or less quadrate, article 10 transverse; articles 5 to 10 decreasing in relative lengths apically.

Mouthparts.—Labrum (Figs. 117, 118) with epipharyngeal area with medial pores very small, rather distantly separated in medial longitudinal sensory field. Mandibles (Fig. 119) with abcondylar molar patch of denticles moderate sized, molar denticles relatively more dispersed than other *Bolitocharina*. Maxilla (Figs. 120, 121) with teeth on apical 0.25 of lacinia arranged in a single row of rather widely dispersed teeth (Fig. 121);

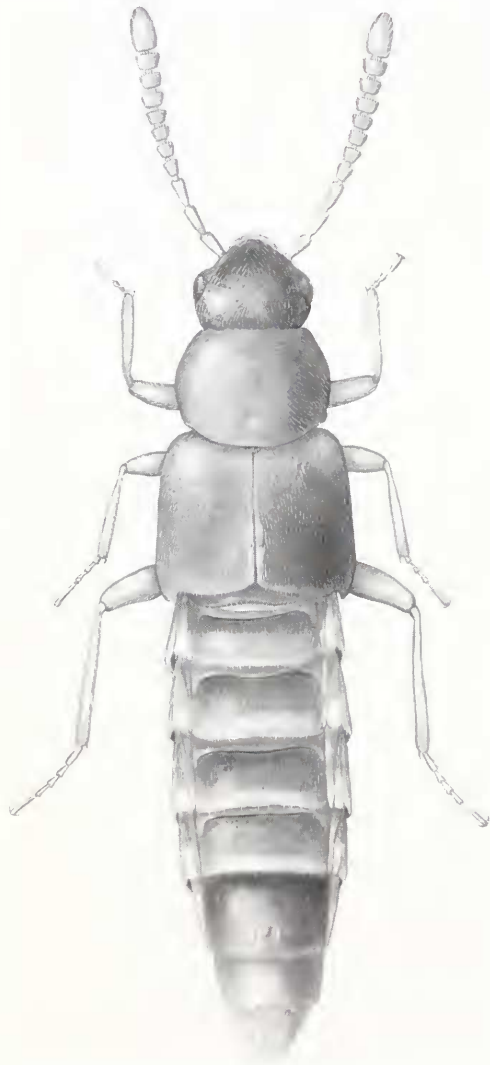


Fig. 115. *Hongophila arizonica* n. sp. Habitus. Length = 3.2 mm.

apex of galea with 6 to 7 rows of unmodified (setose) setae. Labium (Fig. 122) typical of subtribe; ligula with pair of sensory setae very minute; two medial setae present on prementum, bases arranged one directly behind the other, setal insertions close; medial pseudopore field narrow, without pseudopores.

Thorax.—Pronotum broad, transverse, 1.4 times as wide as long in known species, very slightly convex in dorsal outline; about as wide at base as base of clytra; postero-lateral angles slightly angulate but not sharply pointed; base broadly rounded, only very slightly bisinuate basally; punctures small, round, numerous, densely and uniformly distributed; microsetae dense, fine; microsculpture reticulate. Elytra with postero-lateral angles slightly sinuate; punctures small, densely distributed, round, setation fine, densely distributed. Wings with moderate-sized flabellum with 3 to 6 (most with 4) setose lobes (Fig. 124). Hypomeron inflexed posteriorly and deflexed more vertically anteriorly, broadly visible anteriorly; anterior line of hypomeron contacting lateral marginal line of pronotum very near antero-lateral angles of pronotum. Mesosternal medial carina (Fig. 123) present only in anterior 0.2-0.3 of mesosternum. Mesocoxal cavities narrowly separated by meso- and metacoxal processes (Fig. 123); relative lengths mesosternal : isthmus : metasternal processes 5.5 : 0.5 : 3.5 in known species; apex of mesosternal process narrow, broadly pointed; apex of metasternal process acutely rounded. Hind tarsomere I about as long as II and III together.

Abdomen.—Elongate, slender, more or less parallel-sided; terga III-V with moderately deep transverse basal impressions; punctures small, densely distributed, most round, a few broadly lunulate in known species; microsetae numerous, densely distributed, all directed posteriorly; macrosetae inconspicuous. Sterna III-V with very slight transverse basal impressions.

Secondary Sexual Characteristics.—Males: each elytron with small knob near suture and posterior suture slightly flexed dorsally; tergum VII (Fig. 127) with small medial tubercle and larger lateral tubercles; tergum VIII (Fig. 127) broadly and distinctly emarginate, with 5 to 6 moderate to small denticles on each side of midline in emargination; dorsum of tergum VIII with numerous small asperities in known species; sternum VI (Figs. 125, 126) with small medial lobe on posterior margin, lobe without setae; sternum VII (Fig. 125, 126) with concentration of setose glandular pores medially, porose area small, as well as broad band of sensory pores basally; sternum VIII (Fig. 125) with moderate posterior triangular projection, projection without asetose posterior margin.

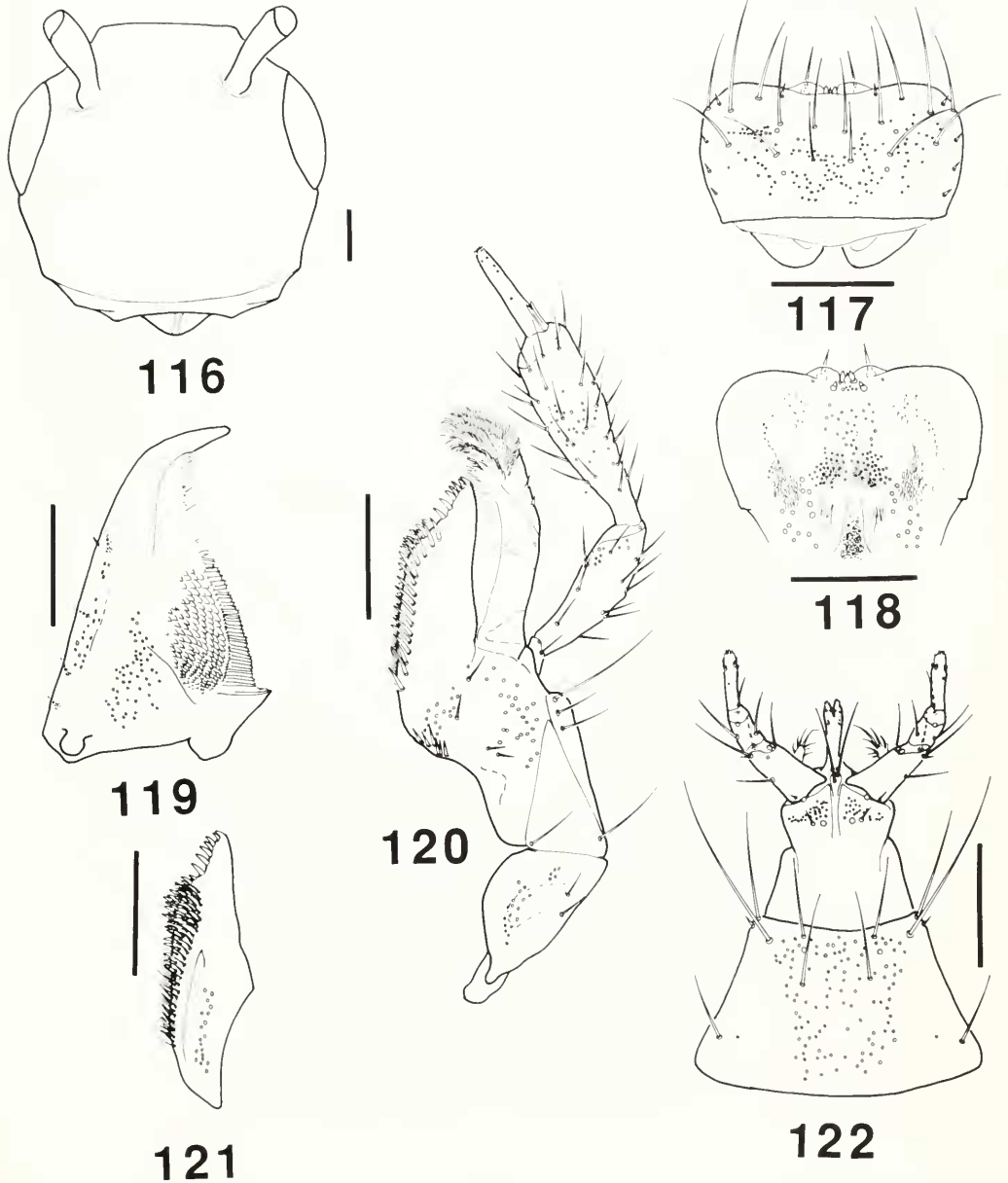
Aedeagus.—Paramere (Fig. 129) with apical lobe of paramerite moderate in length, length about 0.7-0.8 times length of paramerite; setae 1 to 4 of apical lobe long, not clustered near apex. Aedeagus (Fig. 128) with apical process elongate,

slender; internal sac with prominent pair of spinose and recurved sclerotized plates; flagellum moderately long, tapered to an acute apex.

Spermatheca (Figs. 130, 131).—Basal bulb elongate, apex rounded; neck bent at angle of about 30° (Fig. 131); spermathecal tube membranous, very long and convoluted (Fig. 130). Vaginal

sclerotization very slight, only present as inconspicuous arc of sclerotized cuticle.

Discussion.—The genus *Hongophila* is known from only a single species (*H. arizonica* n. sp., see below) which occurs in the mountain systems of Arizona and New Mexico. I have seen specimens of at least two undescribed species which should



Figs. 116-122. *Hongophila arizonica* n. sp. 116, Head, dorsal aspect. 117, Labrum, dorsal aspect. 118, Labrum, epipharyngeal aspect. 119, Mandible, ventral aspect. 120, Maxilla, ventral aspect. 121, Lacinia of maxilla, dorsal aspect. 122, Labium, ventral aspect. (Scale line = 0.1 mm.)

be placed in this genus from the State of Oaxaca in Mexico.

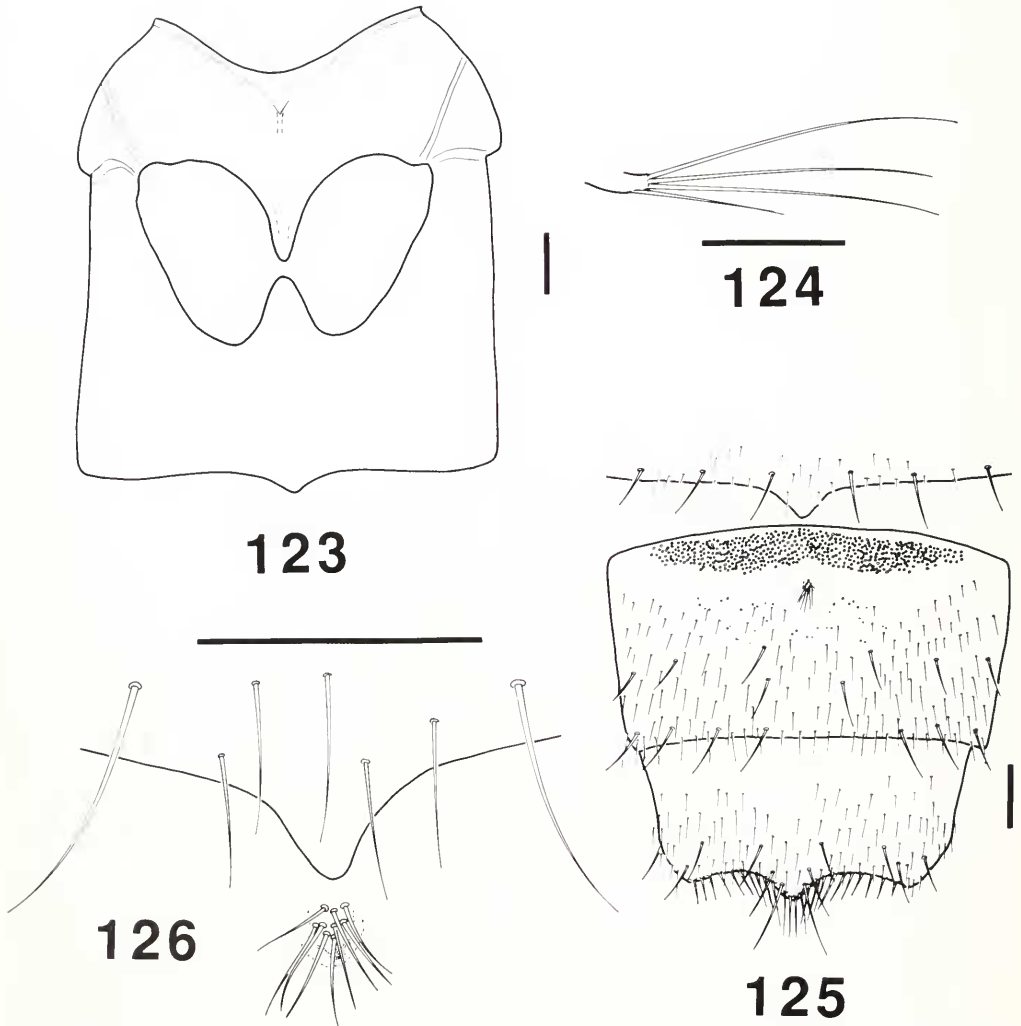
The phylogenetic position of *Hongophila* is somewhat problematic. Those analyses that weight sternal secondary sexual features heavily (Figs. 2, 5) place *Hongophila* as the primitive sister group to *Pleurotobia* + *Bolitochara*. However, unweighted analyses either fail to resolve the position of *Hongophila* (Figs. 1, 3) or place it as an independent basal lineage of bolitocharines (Fig. 4).

Members of *Hongophila* are superficially similar to those of *Neotobia* new genus, but these two genera are not closely related.

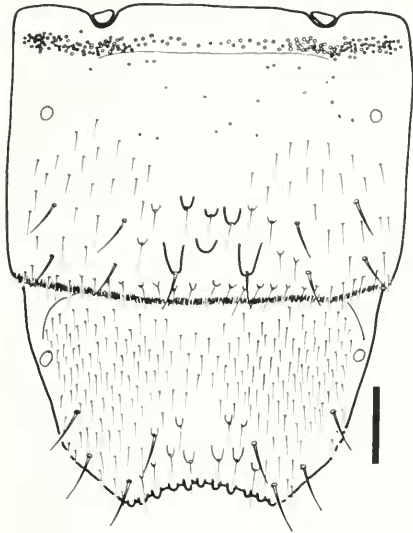
Hongophila arizonica Ashe, new species

(Figs. 115-131)

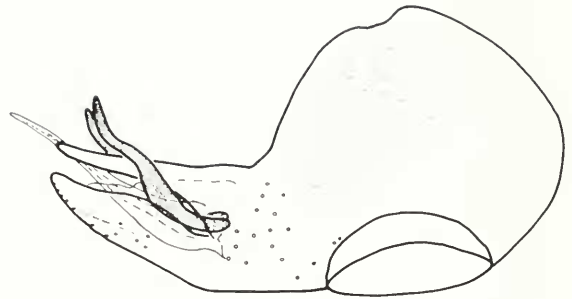
Description (Fig. 115).—Length 2.8-3.5 mm. Body color reddish brown to brown with head slightly darker brown in some specimens, and external basal angles of elytra and posterior margins of abdominal segments III-VI lighter; antenna reddish brown with apical article lighter; legs light brown. Body covered with moderately dense pile of short, fine hairs; punctation very fine, moderately dense. Head, pronotum, and elytra with moderately developed reticulate



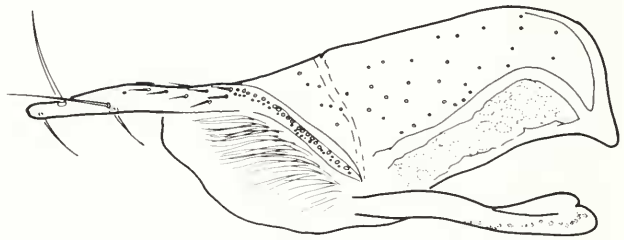
Figs. 123-126. *Hongophila arizonica* n. sp. 123, Meso-metasternum. 124, Flabellum of wing. 125, Male sternal features, posterior margin of sternum VI and sterna VII-VIII. 126, Male, detail of setose lobe on posterior margin of sternum VI and concentration of setose pores on sternum VII. (Scale line = 0.1 mm.)



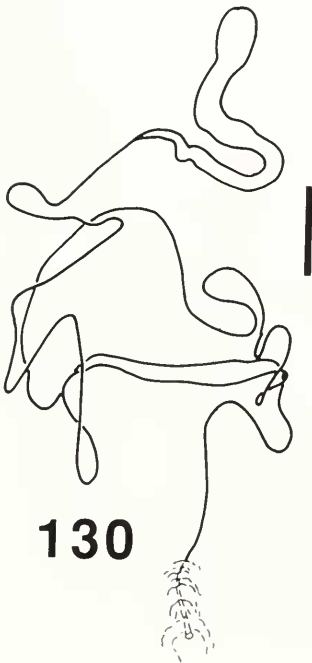
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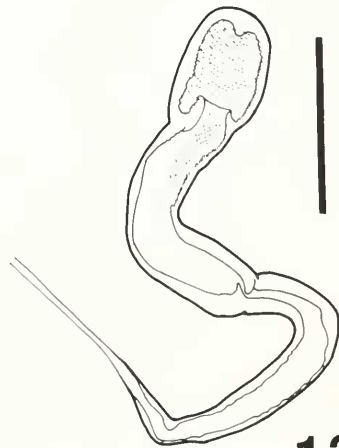
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Figs. 127-131. *Hongophila arizonica* n. sp. 127, Male, terga VII-VIII. 128, Male, median lobe of aedeagus, lateral aspect. 129, Paramere of aedeagus, external aspect. 130, Spermatheca, outline showing long, convoluted spermathecal duct. 131, Spermatheca, detail of basal bulb. (Scale line = 0.1 mm.)

microsculpture; reticulate microsculpture moderately developed to obsolete on abdomen, abdomen slightly shining, with characteristics of the genus.

Male Secondary Sexual Characteristics.—As in Figures 125, 126, 127.

Aedeagus.—As in Figures 128, 129.

Spermatheca.—As in Figures 130, 131.

Type.—Holotype, male, with labels as follows: "USA: Arizona, Coronado National Forest, Chiricahua Mountains, Rustler Park, 16 July 1976, J. S. Ashe, ex polypore, coll. no. 245," "HOLOTYPE, *Hongophila arizonica* Ashe, desig. J. S. Ashe, 1991." Deposited in the Snow Entomological Museum, University of Kansas, Lawrence, Kansas.

Paratypes.—97. ARIZONA: 2 (on microslides), Apache Co., Apache National Forest, Big Lake, 3-VIII-1976, J. S. Ashe, ex polypore on conifer log (SEM); 17, type locality, 27-VII-1983, J. S. Ashe, ex *Hirchioporus abietinus* (1 pinned, 3 on microslides), ex *Fomitopsis pinicola* (2), ex *Armillariella* sp. on conifer stumps (1), ex *Xeromphalina campinella* (1) (FMNH, SEM); 2, Huachuca Mountains, Carr Canyon, 2150 m, 23-VII-1976, J. M. Campbell (CNC); 1, Huachuca Mountains, Miller Canyon, 2190-2380 m, 4-VIII-1979, A. Smetana (CNC); 2, Coconino Co., Flagstaff, no date or collector (CAS); 4, Navajo Co., Sitgraves National Forest, 47.8 mi. E. Payson, hwy. 260, 6-VIII-1983, ex Cortinariaceae, J. S. Ashe (SEM, FMNH); 16 (4 on microslides), Pima Co., Coronado National Forest, Santa Catalina Mountains, Mt. Lemmon Ski Area, 2590 m, 21-VII-1983, ex *Fomitopsis pinicola* (FMNH, SEM); 1, same, ex *Fomitopsis cajanderi* (FMNH); 4, same, ex *Hirchioporus abietinus* (FMNH, SEM), 4 (2 on microslides), same, ex *Flammulina velutipes* (FMNH); 16 (3 on microslides), same locality, 22-VII-1983, ex *Fomitopsis pinicola* (FMNH, SEM); 1, same locality and date, ex *Fomes fomentarius* (FMNH); 5, same locality, 24-VII-1983, ex *Fomitopsis pinicola* (FMNH, SEM); 9, same locality and date, ex *Hirchioporus abietinus* (FMNH, SEM); 3, same locality and date, ex *Pleurotus* sp. (FMNH); 2, same locality and date, ex leathery polypore on aspen log (FMNH); 1, same locality, 25-VII-1983, ex crustose polypore on aspen log (FMNH). NEW MEXICO: 1, state label only (CAS); 2, Lincoln Co., Cibola National Forest, S. slope Gallinas Peak, Red Cloud Campground, 3-VIII-1983, J. S. Ashe, ex *Sparassis radicata* (FMNH); 15 (6 on microslides), Lincoln Co., Lincoln National Forest, White Mountains, 3.2 mi. W. Alta, rd. 532, 2-VIII-1983, J. S. Ashe, ex *Ganoderma tsugae* (FMNH, SEM); 1, same except ex rotting *Paxillus* (?) (FMNH); 1, Otero Co., Cloudcroft, 8-VII-1903, Knaus (CAS); 1, San Miguel Co., Povenis, no date or collector (CAS); 3 (1 on microslide), Socorro Co., Cibola National Forest, San Mateo Mountains, 15.1 mi. S. hwy. 60 on 62, 1-VIII-1983, J. S. Ashe, ex *Clavaria* sp. (FMNH, SEM).

Distribution.—Mountain systems of the southwestern United States. Known from the Chiricahua, Huachuca, Santa Catalina Mountains, as well as the Flagstaff area, in Arizona, and the Gallinas Peak, White, San Mateo and Sacramento Mountains in New Mexico.

Bionomics.—Adults are primarily associated with polypores of the genera *Formitopsis*, *Fomes*, *Ganoderma*, and *Hirchioporus*. However, they have also been collected on ligniferous gilled mushrooms of the genera *Pleurotus*, *Flammulina*, *Xeromphalina*, and *Armillariella*, and the coral mushroom *Clavaria*. Adults have been collected only in July and August. Larvae have not been collected.

Discussion.—*Hongophila arizonica* is the only bolitocharine known to occur in the southwestern United States. This unique range as well as the distinctive color pattern and sexual features of adults are sufficient to distinguish this from all other North American species. However, two undescribed species of *Hongophila* from Mexico can be distinguished from *H. arizonica* primarily by aedeagal features.

Neotobia Ashe, new genus

(Figs. 132-146)

Type species *Neotobia alberta* Ashe.

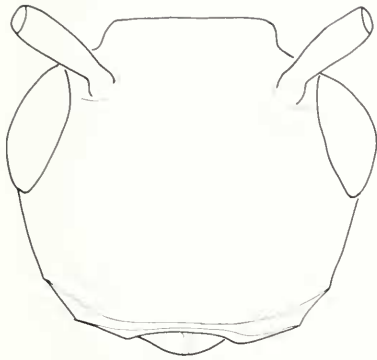
Diagnosis.—Member of *Neotobia* may be recognized by the combination of: eyes moderately large, length 1.2-1.3 times length of temples; head not at all narrowed behind the eyes, neck absent (Figs. 132); at least some antennomeres 5 to 10 elongate; pronotum moderately transverse, 1.35-1.4 times as wide as long, not noticeably narrower at base than base of elytra; hypomeron inflexed to near horizontal plane basally and deflexed more vertically anteriorly, anterior half moderately visible in lateral aspect; mesocoxal cavities moderately separated by intercoxal processes (Fig. 139), mesosternal processes moderately broad, acutely rounded apically; terga III-V (VI slightly) with moderately deep transverse basal impressions; sterna III-V with very faint transverse basal impressions; male sternum VI without medial lobate projection on posterior margin; male sternum VII (Fig. 141) with broad band of numerous sensory pores basally, without concentration of setose pores medially; triangular projection of male sternum VIII (Fig. 141) with asetose posterior margin; median lobe of aedeagus (Fig. 146) with apical process bifid, slender, without sclerotized plates on internal sac, flagellum tubular. As above (see diagnosis of *Hongophila*), members of *Neotobia* are difficult to confidently separate from *Hongophila* without examination of male secondary sexual and aedeagal characteristics.

Description.—Lengths of adults of known species 3.0-4.2 mm. Body somewhat robust, linear, parallel-sided, rather convex in cross section. Surface sculpture markedly reticulate through-

out, surface not shiny. Body microsetae fine, dense, more or less uniformly distributed; punctures small, dense, uniformly distributed. Macrosetae inconspicuous.

Head (Fig. 132).—Broad, transverse, slightly

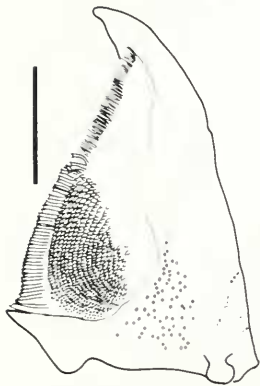
less broad than apex of pronotum. Head not narrowed behind eyes, neck absent. Integumental microsculpture markedly reticulate. Punctures very small, round, densely distributed. Microsetae directed medially and anteriorly. Eyes mod-



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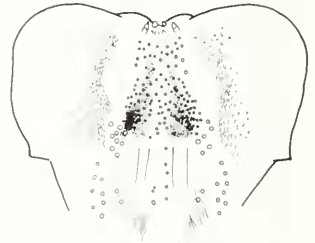
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Figs. 132-138. *Neotobia alberta* n. sp. 132, Head, dorsal aspect. 133, Labrum, dorsal aspect. 134, Labrum, epipharyngeal aspect. 135, Mandible, ventral aspect. 136, Maxilla, ventral aspect. 137, Lacinia of maxilla, dorsal aspect. 138, Labium, ventral aspect. (Scale line = 0.1 mm.)

erately large, length 1.2-1.3 times as long as temples. Infraorbital carina markedly developed, complete. Antenna elongate, very slightly incrasate toward apex; article 4 slightly elongate, similar to 1 to 3 in sculpture and setation; article 5 elongate; article 10 slightly elongate or more or less quadrate; antennal articles 5 to 10 about equal in relative lengths in known species.

Mouthparts.—Labrum (Figs. 133, 134) with epipharyngeal region with medial pores small, scattered, not numerous, evenly dispersed in longitudinal sensory field. Mandibles (Fig. 135) with abcondylar molar patch of denticles large, denticles very small, densely arranged. Maxilla (Figs. 136, 137) with teeth in apical 0.25 of lacinia arranged in a single row (Fig. 137); apex of galea with 10 to 12 rows of small, unmodified (setose) setae. Labium (Fig. 138) typical of subtribe; ligula with pair of sensory setae large; 2 medial setae of prementum present, arranged one directly behind the other, insertions moderately separated; medial pseudopore field narrow, without pseudopores.

Thorax.—Pronotum moderately broad, transverse, 1.35-1.4 times as wide as long, convex in dorsal outline, almost as wide at base as base of elytra; postero-lateral angles slightly angulate but not acutely pointed; base not bisinuate; punctures small, round, numerous; microsetae fine, densely and uniformly distributed; integumental microsculpture markedly reticulate. Elytra with postero-lateral angles moderately sinuate; punctures small, densely distributed, broadly lunulate in form; microsetae fine, densely and uniformly distributed. Wings each with moderately large flabellum with 6 to 8 setose lobes (Fig. 140). Hypomeron inflexed posteriorly and deflexed more vertically anteriorly, broadly visible in lateral aspect anteriorly; anterior line of hypomeron contacting marginal line of pronotum very near antero-lateral angles of pronotum. Mesosternal medial carina distinct, present only in anterior 0.2-0.25 of mesosternum (Fig. 139). Mesocoxal cavities moderately separated by meso- and metasternal processes (Fig. 139); relative lengths of mesosternal : isthmus : metasternal processes of known species 6 : 1 : 3; apex of mesosternal process obtusely pointed; apex of metasternal process broadly rounded. Hind tarsomere I about as long as II and III together.

Abdomen.—More or less robust and parallel-sided. Terga III-V (VI slightly) with moderately deep transverse basal impressions; punctures very small, numerous, densely distributed; microsetae on basal terga directed posteriorly; macrosetae inconspicuous. Sterna III-V with very faint transverse basal impressions.

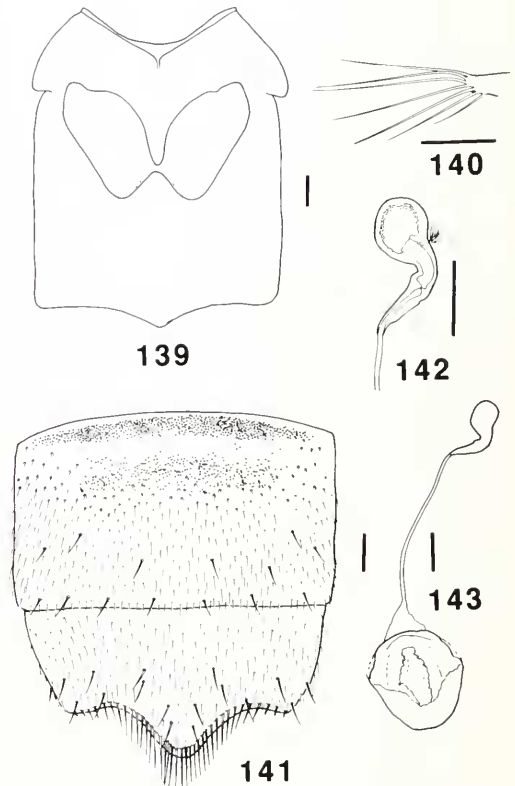
Secondary Sexual Characteristics.—Males: elytra without knob, tubercle or carina near suture, posterior 0.3 of sutural area of each slightly deflexed dorsally in some; tergum VII (Fig. 144) with large median tubercle; tergum VIII (Fig. 144) broadly and distinctly emarginate posteriorly, with 4 to 5 moderately developed denticles

on each side of midline in emargination; dorsum of tergum VIII with small median tubercle; sternum VI without small medial lobe on posterior margin; sternum VII (Fig. 141) with broad band of sensory pores basally (visible in microslide preparations), without medial concentration of setose glandular pores, sternum VIII (Fig. 141) with prominent posterior triangular projection, projection with asetose posterior margin.

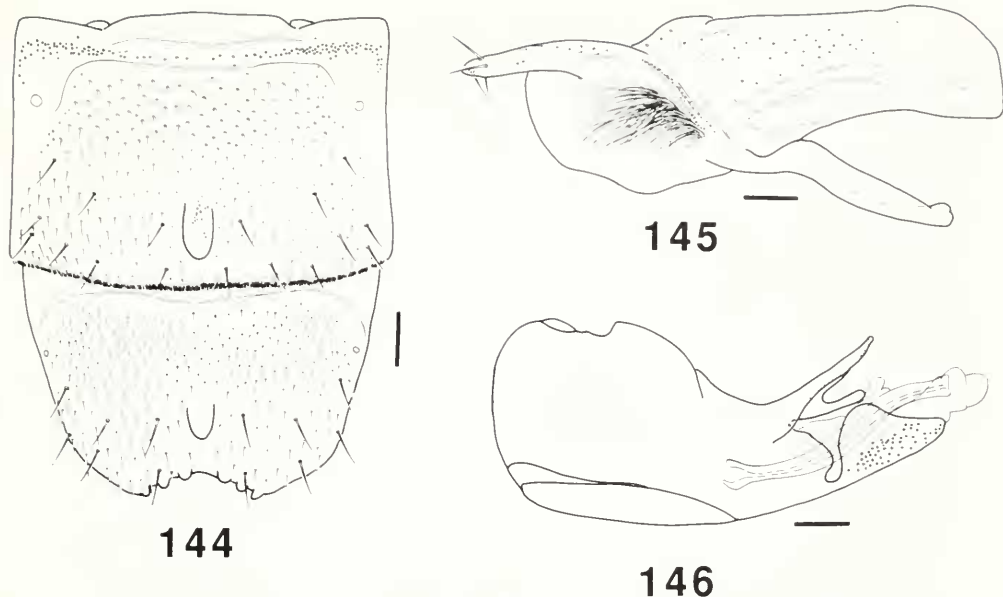
Aedeagus—Paramere (Fig. 145) with apical lobe of paramerite moderate in length, length about 0.5-0.6 times as long as paramerite; setae 1-4 of apical lobe short, clustered near apex of lobe. Aedeagus (Fig. 146) with apical lobe bifid; internal sac without sclerotized internal plates; flagellum long, tubular.

Spermatheca (Fig. 143).—Basal bulb simple, apex rounded; neck bent at angle of about 30°; spermathecal tube membranous, straight. Vaginal sclerotization well developed, present as complete circle of sclerotized cuticle.

Discussion.—The genus *Neotobia* is known from



Figs. 139-143. *Neotobia albata* n. sp. 139, Meso-metasternum. 140, Flabellum of wing. 141, Male, sterna VII-VIII; 142, Female, spermatheca, detail of basal bulb. 143, Female, spermatheca outline showing spermathecal duct and vaginal sclerotization. (Scale line = 0.1 mm.)



Figs. 144-146. *Neotobia alberta* n. sp. **144**, Male, terga VII-VIII. **145**, Male, paramere of aedeagus, external aspect. **146**, Male, median lobe of aedeagus, lateral aspect. (Scale line = 0.1 mm.)

only a single newly described species (*N. alberta* n. sp., see below) which occurs in the northern regions of North America from the Canadian Rockies eastward.

Phylogenetically, *Neotobia* appears to be most closely related to *Phymatura*, though members of *Neotobia* are quite different from those of *Phymatura* in general body form and aedeagal structures.

Members of *Neotobia* are superficially similar to those of *Hongophila*. This similarity is primarily due to retention of a similar array of plesiotypic characters in both genera. They share few derived features and do not appear to be closely related.

Neotobia alberta Ashe, new species
(Figs. 132-146)

Description.—Length 3.0-4.2 mm. Body color light reddish brown with head, pronotum, mesometasternum and abdominal segments VI-VII darker, black, piceus or dark brown. Elytra uniformly light reddish brown. Legs, antennae and mouthparts light brown. Body covered with moderately dense pile of fine hairs; punctation very fine, moderately dense; with moderate to distinct reticulate microsculpture throughout, integuments not markedly shining. With characteristics of the genus.

Male Secondary Sexual Characteristics.—As in Figures 141, 144.

Aedeagus.—As in Figures 145, 146.

Spermatheca.—As in Figure 143.

Type.—Holotype, male, with labels as follows: "CANADA: Alberta, George Lake, 53°57'N 114°06'W, 1 June 1980, J. S. Ashe, ex *Polystic-*

tus," "HOLOTYPE, *Neotobia alberta* Ashe, desig. J. S. Ashe, 1991." Deposited in the Snow Entomological Museum, University of Kansas, Lawrence, Kansas.

Paratypes.—26. 1, same data as holotype (SEM); 5, CANADA, Alberta, George Lake, 53°57'N 114°06'W, 22 August, 1979, J. S. Ashe (SEM, dissected on microslides); 2, same except 9 August 1980 (SEM, on microslides); 5, Alberta, Edmonton, south bank North Saskatchewan River, 12 July 1981, J. S. Ashe, ex *Polyporus picipes* (SEM, 1 pinned, 4 on microslides); 1, Alberta, Elk Island National Park, 7-IX-1980, J. S. Ashe, ex polypore mushroom (SEM, on microslide); 2, E. Ontario, 1887 (CNC); 1, Manitoba, Winnipeg, Hanham (CAS); 1, Montreal (CAS). USA. 1, New Hampshire, Grafton Co., Franconia Notch, 6-VIII-1951, mushrooms, C. Seevers (FMNH); 1, "ME" (= Maine?), Frost (CAS); 7, Wisconsin, Ashland Co., Chequamegon National Forest, 15 mi. W. Mellen, 19-26-VII 1947, C. F. Seevers, ex mushrooms (FMNH, SEM).

Distribution.—Northern North America from the Rockies eastward. Known from Alberta, Manitoba, Ontario and Quebec in Canada, and Maine (?), New Hampshire, and Wisconsin in the United States.

Bionomics.—Adults are primarily found on polypore mushrooms, especially members of the genera *Polyporus* and *Coriolus* (Ashe, unpubl. data) from July through September. Larvae have been found in association with adults on *Polyporus picipes* in July (Ashe, unpubl. data).

Discussion.—As the only known species in the genus *Neotobia*, *N. alberta* can be identified by use of the generic key. In addition, among North American bolitocharines, specimens of *N. alberta* are very easily recognized by their relatively large size, northern distribution, distinctive color pattern (see above), and unique aedeagus and spermatheca.

Austrasilida Ashe, new genus
(Figs. 147-159)

Type species *Austrasilida zealandica* (Cameron) (from *Sternotropa zealandica* Cameron, 1947, p. 726-727).

Diagnosis.—Members of *Austrasilida* can be recognized by: small size, adult length 1.5-2.0 mm; eye length about equal to length of temples; head not at all narrowed behind eyes, neck absent (Fig. 147); antenna short, incrassate, with antennomeres 5 to 10 moderately to strongly transverse; maxillary lacinia with large patch of spines forming a large brush apically (Figs. 150, 151); ligula of labium short and bifid to base (Fig. 153); pronotum strongly transverse, 1.5 times as wide as long, as wide at base as base of elytra; hypomeron inflexed into horizontal plane throughout, only very narrowly visible in lateral aspect; mesosternum with medial longitudinal carina complete to apex of mesosternal process; mesocoxal cavities broadly separated by intercoxal processes (Fig. 154), mesosternal process broad and broadly rounded apically; hind tarsomere I only slightly longer than II; abdominal terga III-IV with at most only slight transverse basal impressions; sterna not basally impressed; male sternum VI without medial lobate projection on posterior margin; male sternum VII (Fig. 155) with broad band of sensory pores basally, without medial concentration of setose sensory pores; triangular projection of posterior margin of sternum VIII (Fig. 155) with very slight asetose margin at apex; median lobe of aedeagus (Fig. 158) with apical process large, tentlike, internal sac without sclerotized plates, flagellum tapered to a point apically. Known only from New Zealand.

Description.—Length of adults 1.5-2.0 mm. Body relatively broad, somewhat robust in build, slightly narrowed anteriorly and posteriorly. Surface sculpture absent, integument strongly shiny. Body microsetae fine, rather stiff, moderately densely and uniformly distributed. Macrosetae inconspicuous.

Head (Fig. 147).—Broad, transverse, almost as wide as apex of pronotum. Head not narrowed behind eyes, neck absent. Integumental sculpture absent, surface shiny. Punctures moderate sized, round; microsetae rather stiff, directed mostly anteriorly. Eye length about equal to length of temple. Infraorbital carina markedly developed, complete. Antenna short, distinctly incrassate toward apex; article 4 transverse, similar to articles 1 to 3 in sculpture and setation; article 5 transverse; article 10 very transverse; articles 5 to 10 decreasing in relative lengths apically.

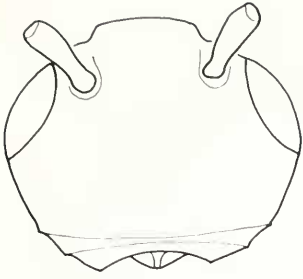
Mouthparts.—Labrum (Figs. 148, 149) with epipharyngeal area with medial pores very minute antero-medially and mostly absent elsewhere in median longitudinal sensory field. Mandibles (Fig. 152) with abcondylar molar patch of denticles large, denticles large, numerous, dense. Maxilla (Figs. 150, 151) with teeth on apical 0.25 arranged into a dense, compact patch of numerous teeth (Fig. 151); apex of galea with 5 to 6 rows of unmodified (setose) setae. Labium (Fig. 153) different from those of other members of subtribe; ligula short, divided almost to base, without pair of sensory spines; two medial setae present, arranged transversely (one beside the other), bases widely separated; medial pseudopore field broad, with 5 to 6 pseudopores.

Thorax.—Pronotum broad, transverse, about 1.5 times as wide as long, moderately convex in dorsal outline; almost as wide at base as base of elytra; postero-lateral angles moderately angulate, not sharply pointed; slightly bisinuate basally; punctures moderately large, close, densely arranged; microsetae dense, stiff; integument without microsculpture. Elytra with postero-lateral angles moderately sinuate; punctures moderately large, round, densely distributed; microsetae dense, stiff. Wings without apparent flabellum, without setose lobes. Hypomeron inflexed into horizontal plane, only very narrowly visible in lateral aspect. Mesosternal medial carina very prominent (Fig. 154), complete to apex of process. Mesocoxal cavities widely separated by meso- and metasternal processes (Fig. 154); relative lengths mesosternal : isthmus : metasternal processes 3.5 : 0 : 2 in known species; apex of mesosternal process rounded; apex of metasternal process broadly rounded. Tarsomere I of hind tarsus short, only about 1.1 times as long as II.

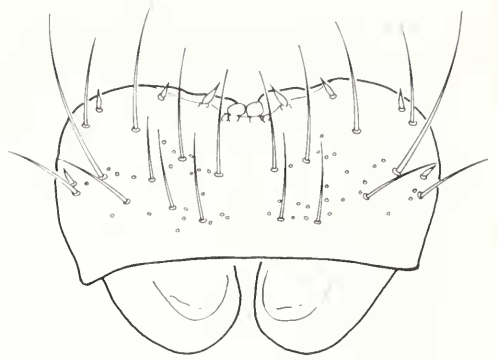
Abdomen.—Slightly tapered from base to obtusely pointed apex; terga III-IV with very slight transverse basal impressions; punctures small, densely distributed; microsetae very fine, densely distributed, oriented obliquely toward midline on first visible tergum; macrosetae present but not large. Sterna III-V without transverse basal impressions.

Secondary Sexual Characteristics.—Males: elytra without carina, knob or tubercle near suture; tergum VII (Fig. 156) with conspicuous spine on each side of midline or spines inconspicuous or absent; tergum VIII (Fig. 156) deeply emarginate posteriorly, with markedly developed spinose processes at each lateral edge of emargination, with 3 to 4 moderately strong spinose processes on each side of midline in emargination; dorsum of tergum VIII without modifications; sternum VI without medial lobe on posterior margin; sternum VII (Fig. 155) with broad band of sensory pores basally (visible in microslide preparations), without concentration of setose glabular pores medially; sternum VIII (Fig. 155) with very slight and broad triangular projection, with asetose posterior margin only at apex of projection.

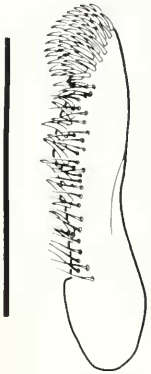
Aedeagus.—Paramere (Fig. 157) with apical



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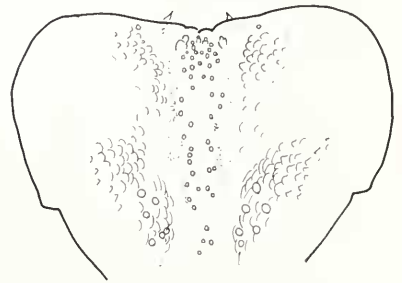
148



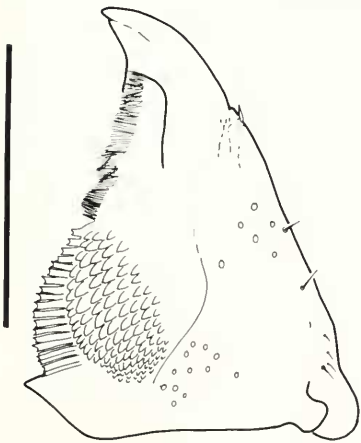
151



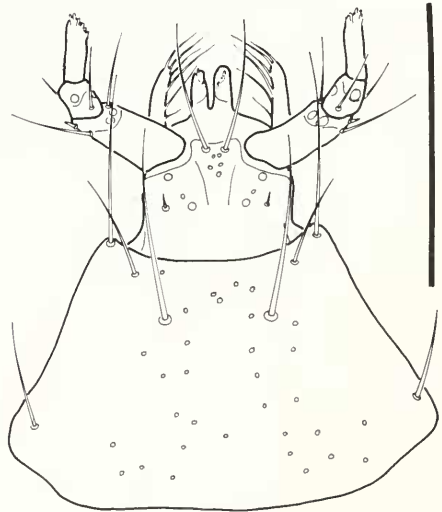
150



149



152



153

Figs. 147-153. *Austrasilida zealandica* (Cameron). 147, Head, dorsal aspect. 148, Labrum, dorsal aspect. 149, Labrum, epipharyngeal aspect. 150, Maxilla, ventral aspect. 151, Lacinia of maxilla, dorsal aspect. 152, Mandible, ventral aspect. 153, Labium, ventral aspect. (Scale line = 0.1 mm.)

lobe of paramerite moderately long, about 0.5 times as long as paramerite; setae 1 to 4 of apical process long, clustered near apex. Aedeagus (Fig. 158) with apical lobe large, tentlike; internal sac without internal sclerotized plates; flagellum long, tubular but tapered to point apically.

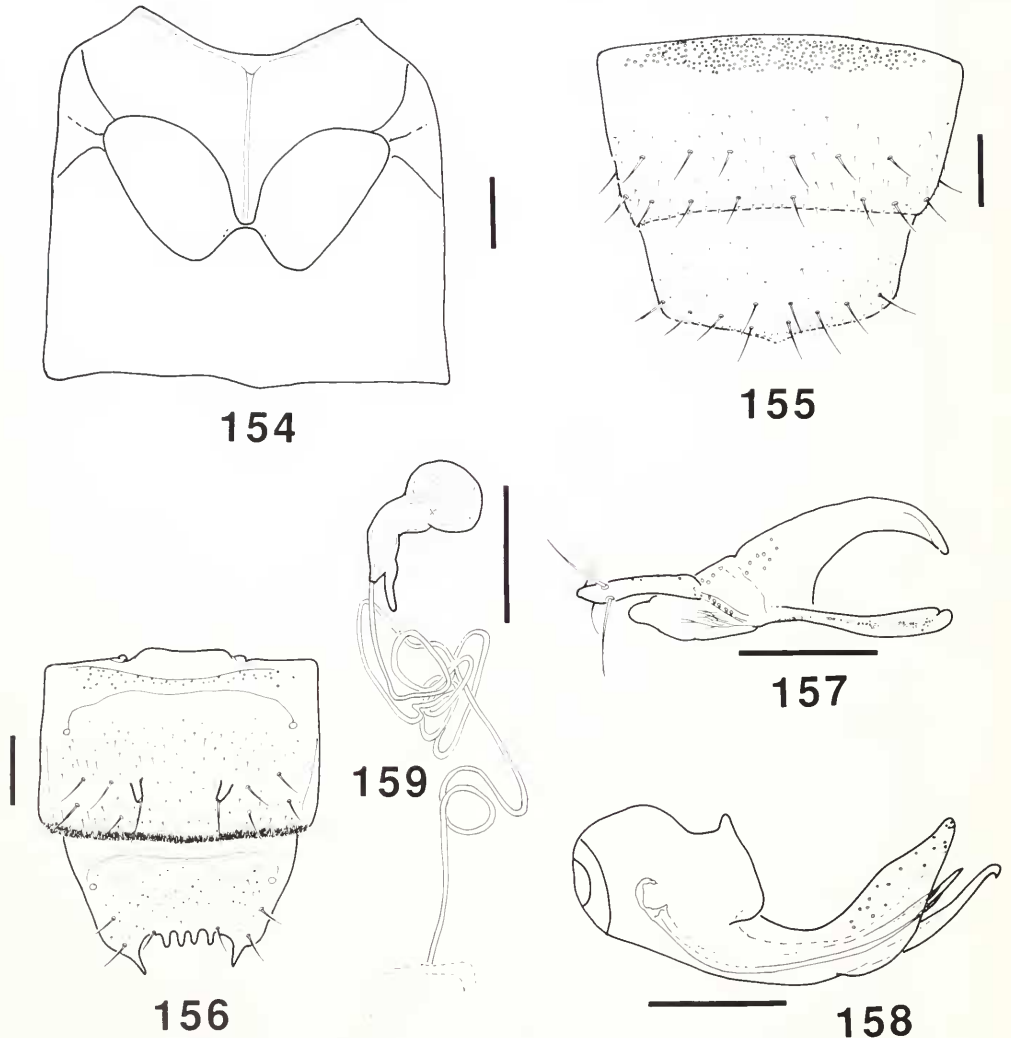
Spermatheca (Fig. 159).—Basal bulb simple, globular, apex rounded; neck bent about 60° from straight; spermathecal tube membranous, straight, very long; vaginal sclerotization very slight to absent.

Discussion.—Cameron (1947) described *Sternotropa zealandica* without providing any explanation about why he placed it in *Sternotropa*. It is clearly not a member of *Sternotropa*, a genus in the

subtribe Gyrophaenina. Furthermore, it is not a member of any other monophyletic bolitocharine genus. Therefore, *S. zealandica* requires a new generic assignment.

As noted elsewhere (see "Choice of Taxa") inclusion of *Austrasilida zealandica* in the subtribe Bolitocharina is problematic. If included, it appears to be most closely related to *Pseudatheta* (Fig. 2). However, its position is not strongly supported by synapomorphies (see "Phylogenetic Analysis"). Also, the phylogenetic structure of the cladogram is substantially affected if *Austrasilida* is not included in the analysis.

Austrasilida could be a very basal member of the subtribe Gyrophaenina. The structure of the



Figs. 154-159. *Austrasilida zealandica* (Cameron). 154, Meso-metasternum. 155, Male, sterna VII-VIII. 156, Male, terga VII-VIII. 157, Male, paramere of aedeagus, external aspect. 158, Male, median lobe of aedeagus, lateral aspect. 159, Female, spermatheca. (Scale line = 0.1 mm.)

“spore brush” on the lacinia of the maxilla and the lateral flange on the spermatheca are apomorphies shared with all gyrophaenines. However, structure of the ligula of the labium and the presence of two medial setae on the prementum are inconsistent with this interpretation. Further resolution of the phylogenetic position of *Australida* must await additional study.

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APPENDIX 1. TAXA OF THE TRIBE HOMALOTINI (= BOLITOCHARINI) AND "RELATED" GROUPS EXAMINED

This list includes homalotine and related taxa which were examined to determine character distributions for outgroup analysis, and were critical in evaluating the monophyly of the subtribe Bolitocharina as presented here. Taxa included here are either traditionally included in the Homalotini or have at one time or another been included in the Homalotini or subtribe Bolitocharina. The monophyly and correct placement of these higher taxa and their included genera and species are outside the range of this study and have not been examined in any comprehensive way. Therefore, the arrangement of taxa in this list should not be taken to be an adequate classification scheme. Representatives of all taxa on this list have been fully dissected, mounted on microscope slides and examined using compound optics.

The letters following each species name indi-

cate whether primary type material (T, holotype or syntype) or other identified specimens (S) were examined. A brief summary of the distribution of each species is given.

TRIBE HOMALOTINI

Subtribe Bolitocharina

(see Appendix 2)

Subtribe Gyrophaenina

(see Ashe, 1984)

Subtribe Homalotina

Anomognathus cribrum Fauv., S, New Guinea

A. cuspidatus Er., S, Europe

Homalota borgeoni Bernh., S, Africa

H. flavomaculata Bernh., S, Africa

H. fuscipennis Cam., S, S.E. Asia

H. intrusa Er., S, South America

H. plana Gyll., S, Europe

H. variventris Kr., S, Ceylon

Thecturota sp., S, North America

Subtribe Leptusina

Euryusa brachelytra Kiesenw., S, Europe

E. castanoptera Kr., S, Europe

E. optabilis Heer, S, Europe

Leptusa alpicola Brancsik, S, Europe

L. angusta Aubé, S, Europe

L. carpathica Weise, S, Europe

L. eximia Kr., S, Europe

L. flavicornis Brancsik, S, Europe

L. granulicauda Eppels., S, Europe

L. hopffgarteni Eppels., S, Europe

L. lombarda Bernh., S, Europe

L. piceata Muls. & Rey, S, Europe

L. oreophila Penecke, S, Europe

L. reitteri Eppels., S, Europe

L. ruficollis Er., S, Europe

L. secreta Bernh., S, Europe

L. tricolor Scriba, S, Europe

Leptusa sp. 1, S, North America

Leptusa sp. 2, S, North America

Leptusa sp. 3, S, North America

Leptusa sp. 4, S, North America

Paraleptusa graeca Bernh., S, Europe

Subtribe Silusina

Diestota angustula Casey, S, USA

D. brasiliانا Bernh., S, Brazil

D. laticornis Sharp, S, Central America

D. luederweldti Bernh., S, Brazil

D. obsoleta Er., S, Central America

D. rufipennis Casey, S, North America

D. testacea Kr., S, S.E. Asia

Elachistarthon ambiguum Notman, S, North America

Neosilusa ceylonica Kr., S, S.E. Asia

Silusa californica Casey, S, W. North America

S. opaca Fenyés, S, W. North America

S. rubra Er., S, Europe

Silusa sp., S, USA

Tachiona deplanata Sharp, T,S, Mexico

T. montevedensis Ashe, T,S, Costa Rica

T. latipennis Ashe, T,S, Panama

Toxoxelia parvipennis Bernh.

Unplaced Homalotini

Caloderina hierosolymitana Sauley, S, Europe

Coenonica puncticollis Kr., S, Ceylon

Gansia varicornis Sharp, S, South America

Heterota plumbea Waterhouse, S, Europe

Ophioglossa araucana Fauv., S, South America

O. cava Sharp, S, South America

Paracyphea asperata Bernh., S, Seychelles

Pseudoplacusa rufiventris Cam., S, S.E. Asia

Trichiusa sp., S, North America

Tribe Autaliini

Autalia impressa Oliv., S, Europe

A. rivularis Grav., S, USA, Europe

A. puncticollis Sharp, S, Europe

Autalia n. sp., S, Costa Rica

Tribe Philotermini

Philoterme pilosus Kr., S, North America

Tribe Phytosini

Actocharis marina Fauv., S, Europe

Bryobiota bicolor Casey, S, W. North America

Dialuota densissima Casey, S, W. North America

D. fulviventris Casey, S, W. North America

Liparocephalus brevipennis Mäklin, S, W. North America

America

Phytosus balticus Kr., S, Europe

P. spinifer Curtis, S, Europe

Thinusa maritima Casey, S, W. North America

Tribe Placusini (see Ashe, 1991)

Placusa atrata Sahlb., S, Europe

P. complanata Er., S, Europe

P. despecta Er., S, USA

P. spinigera Kr., S, Ceylon

P. tachyporoides Walil, S, Europe

P. tacomae Casey, S, W. USA

P. trispinosa Bernh., S, Africa

Euviva cubana Bierig, T,S, Cuba

E. debilis Sharp, S, Central America

E. diazbatesi Ashe & Kistner, T,S, Mexico

E. godmani Sharp, S, Central America

E. nigra Sharp, S, Central America

APPENDIX 2. TAXA OF THE SUBTRIBE BOLITOCCHARINA EXAMINED

Taxa included in the phylogenetic analysis are indicated by an asterisk (*) following the name. Taxa examined which represent synonyms are indicated by placing them in parenthesis below the valid name for the taxon. Specimens of most taxa included on this list were fully dissected and examined on microslides. At least genitalia of all were examined with compound optics.

The letters following each species name indicate whether primary type material (T, holotype or syntype) or other identified specimens (S) respectively were examined. A brief summary of the distribution of each species is given. In this table, genera are listed in the sequence of the descriptive section, and species are ordered alphabetically under each genus.

Bolitochara Mannerheim

(*Ditropalia* Casey)

- B. bella* Maerk.* (from *Ditropalia*), S, Europe
- B. humeralis* (Lucas) (from *Ditropalia*), S, N. Africa, Europe
- B. laufferi* Bernh. (from *Ditropalia*), S, N. Africa
- B. lucida* Grav.*, S, Europe, N. Africa
- B. lunulata* Payk.*, S, Europe
- B. mulsanti* Sharp* (from *Ditropalia*), S, Europe
- B. obliqua* Er.* (from *Ditropalia*), S, Europe
- B. reyi* Sharp, S, Europe
- B. schusteri* Bernh. (from *Ditropalia*), S, Tunis
- B. varia* Erichson (from *Ditropalia*), S, S. Europe, N. Africa

Phymatura Sahlberg

(*Venusia* Casey)

- P. aspericeps* Cam., S, India
- P. blanchardi* (Csy.)* (from *Venusia*), T,S, E. North America
- (*Bolitochara blanchardi* Casey), T,S, E. North America
- (*Venusia laetula* Casey), T, E. North America
- (*Venusia picta* Casey), T, E. North America
- P. brevicollis* Kr.*, S, Europe
- P. intermedia* Cam., S, India
- P. juncunda* Cam.*, S, India
- P. picta* Cam.*, S, India

Pleurotobia Casey

(*Phymaturosibus* Roubal)

- P. magnifica* (Roubal)* (from *Phymaturosibus*), S, Central Europe
- P. trimaculata* (Er.)* (from *Bolitochara*), S, E. North America
- (*P. suturalis* Casey), T, E. North America
- (*P. texana* Casey), T, E. North America
- (*P. tristigma* Casey), T, E. North America
- P. n. sp. A**, S, Central North America
- Pseudatheta* Cameron
- P. elegans* Cam.*, S, S.E. Asia

Silusida Casey

- S. marginella* Casey*, T,S, E. North America
- (*S. nanella* Casey ?), specimens not found

Stictalia Casey

- S. arcuata* Casey, T, W. North America
- S. aspera* Casey, T, W. North America
- S. bakeri* Casey*, T,S, W. North America
- S. brevicornis* Casey*, T,S, W. North America
- S. carlottae* Casey, T,S, W. North America
- S. californica* Casey*, T,S, W. North America
- S. collaris* Casey, T, W. North America
- S. densicollis* Casey, T, W. North America
- S. laxicornis* Casey, T, W. North America
- S. minor* Casey*, T,S, W. North America
- S. nigrina* Casey*, T,S, W. North America
- S. notata* (Mäklin) (from *Bolitochara*), S, W. North America
- S. obsolescens* Casey, T,S, W. North America
- S. rugipennis* Casey*, T,S, W. North America
- S. unicolor* (Fenyés) (from *Bolitochara*), T,S, W. North America
- S. n. sp. 1*, S, W. North America
- S. n. sp. 2*, S, W. North America
- S. n. sp. 3**, S, W. North America
- S. n. sp. 4*, S, W. North America

S. n. sp. 5, S, W. North America

*S. n. sp. 6**, S, W. North America

Hongophila Ashe (new genus)

H. arizonica Ashe* (new species), T,S, S.W. USA

Neotobia Ashe (new genus)

N. alberta Ashe* (new species), T,S, N. North America

Austrasilida Ashe (new genus)

A. zealandica (Cam.)* (from *Sternotropa*), S, New Zealand

APPENDIX 3. STATES AND ADDITIVE BINARY CODING OF CHARACTERS USED IN CLADISTIC ANALYSIS OF TAXA OF SUBTRIBE BOLITOCHARINA

Character	States	Binary Coding
1. Head: shape		
0. distinctly broader than long (width: length 1.1 or greater)		0000
1. more or less oval, slightly broader than long (width:length ratio >1.0<1.1)		0001
2. more or less quadrate (width:length ratio about 1.0)		0011
3. slightly elongate (width:length ratio <1.0>0.9)		0111
4. distinctly elongate (width:length ratio 0.9 or less)		1111
2. Head: infraorbital carina		
0. infraorbital carina strong to moderate, complete		0
1. infraorbital carina absent except faintly near maxillary insertion		1
3. Head: neck		
0. absent		00
1. present, slightly developed (neck wider than 2/3 head width)		01
2. present, distinct to very distinct (neck 2/3 to 1/2 head width)		11
4. Head: setation		
0. setae directed medially in postero-lateral areas and anteriorly in midline and anterior portions of head.		00
1. most to all head setae directed anteriorly		10
2. most to all head setae directed medially		01
5. Pronotum: width:length ratio		
0. width:length ratio 1.4 or greater		00
1. width:length ratio >1.2<1.4		01
2. width:length ratio 1.2 or less		11
6. Pronotum: width relative to elytra width		
0. almost as wide as base of elytra.		0
1. distinctly narrower than elytra		1
7. Pronotum: microsculpture		
0. slightly to moderately reticulate.		00
1. obsolete reticulate		01
2. smooth and shiny, without microsculpture		11
8. Wing: number of setose projections on flabellum		
0. 10-13		0000
1. >4≤8		0001
2. ≥3≤4		0011

3. >1 <3	0111	17. Labium, ligula: pair of sensory spines	
4. 1 or less	1111	0. pair of large sensory spines on ligula	00
9. First visible abdominal tergum: direction of setae		1. pair of sensory spines on ligula minute to small	01
0. all directed posteriorly	0	2. sensory spines absent from ligula	11
1. some setae oblique or transverse	1	18. Labium: medial setae	
10. Mesosternum: medial carina		0. medial setae side by side, bases close to contiguous	0000
0. medial carina strong, complete to apex of mesosternal process	00	1. medial setae side by side anterior to medial pseudopore field, bases distant	1000
1. medial carina strong, but fading in apical 0.5-0.3 of mesosternum	01	2. medial setae arranged one laterally behind the other	0001
2. medial carina strong but present only on basal 0.2-0.3 of mesosternum	11	3. medial setae arranged one directly behind the other, bases close	0011
11. Intercoxal processes: degree of separation of middle coxae		4. medial setae arranged one directly behind the other, bases distant	0111
0. coxae narrowly separated (separation less than 0.15 total length meso- and metasternal processes)	00	19. Labium: medial pseudopore field	
1. coxae moderately separated (separation >0.15 <0.35 times combined length of processes)	01	0. medial pseudopore field narrow, pseudopores present in linear array	00
2. coxae widely separated (separation greater than 0.35 times combined length of processes)	11	1. medial pseudopore field broad, pseudopores present in more or less rectangular array	10
12. Intercoxal processes: isthmus present or absent		2. medial pseudopore field narrow, pseudopores absent	01
0. isthmus distinctly present (isthmus length greater than 0.1 times combined length of processes)	00	20. Male secondary sexual char.: elytra, sutural carina	
1. isthmus slight (isthmus length 0.1 to 0.02 times combined length of processes)	01	0. elytra suture not modified	00
2. isthmus virtually to completely absent (processes in contact or separation not greater than 0.02 times combined length of processes)	11	1. each elytron with small knob or tubercle near suture in posterior 0.5	01
13. Antenna: antennomere 4		2. each elytron with distinct and strong carina near suture in posterior 0.5	11
0. similar to antennomeres 5-10	00	21. Male secondary sexual char.: tergum VII	
1. transitional in setation, microsculpture and general shape between antennomeres 1-3 and 5-10	01	0. small to moderate medial tubercle, without lateral scattered asperities	00000
2. similar to antennomeres 1-3	11	1. small to very small medial tubercle, with small to very small lateral asperities	00001
14. Antenna: relative lengths of antennomeres 5-10		2. without medial tubercle, with very faint scattered asperities	00011
0. antennomeres 5-10 distinctly decreasing in relative lengths apically	00	3. with short distinct medial carina	00100
1. antennomeres 5-10 more or less the same in relative lengths	01	4. with very long prominent medial carina	10100
2. antennomeres 5-10 distinctly increasing in relative lengths apically	11	5. with two to three oblique carinae on each side	01100
15. Mandibles: molar denticles		22. Male secondary sexual char.: tergum VIII	
0. denticles in molar region few to numerous, scattered, not densely arranged.	0	0. small to very faint medial tubercle	00000
1. denticles in molar region very numerous, arranged densely in large patch.	1	1. a few minute, scattered asperities	00011
16. Maxillary lacinia: inner apical teeth		2. no modifications	00001
0. one row of teeth on inner face of lacinia in apical 0.25-0.35	000	3. short, medial carina	00100
1. inner face of apical 0.25 of lacinia with one row of teeth more basally and two irregular rows more apically	001	4. prominent long medial carina	01100
2. inner face of lacinia with 3-6 rows of teeth in apical 0.25 with noticeably denser concentration of teeth near apex	011	5. moderate to prominent medial carina with shorter flanking carinae or tubercles	10100
3. lacinia with 3-6 rows of teeth in apical 0.25 with very dense and large concentration of teeth near apex	111	23. Male secondary sexual char.: tergum VIII, denticles in apical emargination	
		0. emargination broad and deep, denticles moderate to robust.	00
		1. emargination broad and shallow, denticles very small to faint	01
		2. emargination very shallow to indistinct, denticles virtually absent to absent.	11
		24. Male secondary sexual char.: sternum VI, lobate projection apico-medially	
		0. small lobate projection absent	00
		1. lobate projection present, glabrous	01
		2. lobate projection present, setose	11
		25. Male secondary sexual char.: sternum VII	
		0. uniform broad band of asetose sensory pores present around base of sternum	

VII, medial setose glandular concentration absent	00	2. very long, tubular	010
1. band of asetose sensory pores around base of sternum VII broad, medial setose glandular concentration present but small.	01	3. moderate length, tapering to sharp apex	100
2. band of asetose sensory pores around base of sternum VII reduced, medial setose glandular concentration present, large	11	30. Female spermatheca: basal bulb shape	
26. Male secondary sexual char.: sternum VIII, apical triangular lobe		0. basal bulb simple, base rounded	00
0. margin of lobe setose to edge	0	1. basal bulb elongate, base rounded	01
1. lobe with distinct asetose margin	1	2. basal bulb simple, with a small knob at base	10
27. Male genitalia: apical lobe of aedeagus		31. Female spermatheca: neck shape	
0. apical lobe large, tentlike	0000	0. neck straight to very slightly bent	00
1. apical lobe slender and elongate	0001	1. neck bent at $>30^\circ$ and $<90^\circ$	01
2. apical lobe slender, rather foot-shaped in lateral aspect	0010	2. neck bent at $>90^\circ$ angle	11
3. apical lobe slender, recurved	0110	32. Female spermatheca: tube structure	
4. apical lobe bifid.	1000	0. tube membranous	0
28. Male genitalia: aedeagus, internal plates		1. tube sclerotized	1
0. internal plates present, plates large, flattened	00	33. Female spermatheca: tube shape	
1. internal plates present, plates spinose and recurved	10	0. tube of moderate length, more or less straight	00
2. internal plates absent	01	1. tube very long and irregularly convoluted	10
29. Male genitalia: median lobe, flagellum		2. tube twisted into 1-3 regular loops.	01
0. moderate length, tubular	000	34. Female sexual char.: vaginal sclerotization	
1. short, tubular	001	0. vaginal sclerotization very light, absent or present as an inconspicuous arc	00
		1. vaginal sclerotization moderate to slight, evident as approximately 0.5 circle of sclerotized area	01
		2. vaginal sclerotization moderate to distinct, sclerotized ring complete or at least 0.75 complete	11